Ryder, (J. A.)

ON THE DEVELOPMENT OF VIVIPAROUS OSSEOUS FISHES AND OF THE ATLANTIC SALMON.

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JOHN A. RYDER.

[EXTRACTED FROM PROCEEDINGS UNITED STATES NATIONAL MUSEUM, 1885, PAGES 128-162, PLATES VI-XII.]

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INTRODUCTORY.

The following paper is intended to give a summary of our knowledge respecting the best known of the truly viviparous osseous fishes characterized by an intrafollicular or intraovarian development. The only memoirs of importance which have not been consulted in the preparation of this series of notes is that by Rathké,* on *Zoarces viviparus*, and that by Duvernoy on *Pœcilia surinamensis*, which is cited at another place.

The preliminary notice published by me on the development of *Gambusia* appeared nearly four years ago, and left the subject in a very incomplete state. What is here added on the anatomy of the embryos and the follicles may, I trust, be of interest to morphologists.

The new observations here recorded on the changes undergone by the embryos of the Ebiotocoids during gestation, relate to the development of the intestine and the vascular supply of the median fins, both of these organs also undergoing other changes which have appeared to the writer to have considerable significance.

Some apology may be necessary for the long extracts which I have incorporated from the paper by Professor Wyman and Dr. Girard's report, but I think the student who wishes to be spared the vexatious task of finding and consulting authorities will be rather gratified than otherwise to find the American contributions to the subject thus brought together.

I.—THE DEVELOPMENT OF ANABLEPS.

Wyman's memoir † on Anableps contains such valuable observations and reflections on the viviparity of fishes that I will here reproduce the most important parts of his paper entire, as follows:

"Extended observations have proved that a large number of species of fishes, belonging to many genera, are truly viviparous, the fœtus passing through a real gestation by the parent before its development is complete. These viviparous fishes may be divided into two groups, according to the position occupied by the embryo during the period of its growth.

"I. In the first group may be arranged those fishes in which *the*

* Bildungs- und Entwickelungsgeschichte des Blennius viviparus oder des Schleimfisches. Abhandl. zur Entwickelungsgeschichte. Zweiter Theil, Erste Abh., pp. 1–68 pls. 5, 4to, Leipsic, 1833.

† Observations on the development of *Anableps Gronovii* (Cuv. & Val.). By Jeffries Wyman, M. D., Bost. Journ. Nat. Hist, vi, 1850–'57, pp. 432–443, pl. xvii.

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ovum leaves the ovary in an undeveloped state, and in which the process of evolution is not commenced until it reaches the lower portion of the oviduct. The species which this group comprises are nearly all, if not all, Plagiostomes. The best known are *Spinax*, *Carcharias*, *Mustelus*, *Galeus*, and *Torpedo.* Although they are usually classified among the lowest of fishes, it is in some of them that the process of reproduction becomes most nearly analogous to that of the highest Vertebrates. Not only does the yelk reach proportions like the yelk of birds, but the yelk-sac itself plays the part of an allantois and forms an organ analogous to a placenta. In Spinax the vessels on the surface of the vitelline sac are brought into close contact with the highly-vascular folds which line the oviducts. But in Carcharias, as Müller has demonstrated in his memoir on the subject, not only is there an approximation of the fœtal and maternal vessels, but the surfaces of the yelk-sac and of the oviduct are both deeply convoluted, and the projections of the one are admitted into and embraced by the concavities of the other, and the opposing surfaces become adherent even. In both Spinax and Carcharias the necessary conditions exist for the reaction of maternal and fœtal blood upon each other, as in the case in the mammalia, but to a much more limited extent.*

"II. In the second group those fishes are comprised in which *the gestation is either wholly or in part ovarian*, the last stages only of the process usually occurring in the oviduct. Among the genera included in this division are *Silurus*,† *Blennius*,‡ *Anableps*,§ *Pœcilia*,|| and *Embiotoca*.¶ In all of these genera impregnation takes place in the ovary, and, as seems probable, while the ovum is still invested with its original envelopes. In Blenny, Rathké has shown, the ovarian gestation having continued about three weeks, that about the end of September the sac ruptures, and that the embryo is discharged into the central cavity of the ovary, which is in fact the oviduct; here the fœtus remains till the beginning of January, when it is born. In Pœcilia the fœtus is liberated and escapes into the oviduct towards the end of gestation. Valenciennes has given several details in relation to the development of *Anableps Gronovii*, made for the most part upon specimens in an advanced stage of fœtation, the smallest embryo being more than an inch long. He

* Dr. John Davy has shown that in Torpedo the embryo is nourished at the expense of materials furnished by the parent, since the mature fœtus weighs more than twice as much as the egg at the time development commenced. Philos. Trans., 1834. *On the Development of the Torpedo.*

† Cuvier et Valenciennes, Hist. Nat. des Poissons, t. i., p. 540, 1828.

‡ Rathké, Mem. sur la Develop. de l'Homme et des Animaux, 2me partie, Leipsic, 1833.

§ Cuv. and Valenciennes, Hist. Nat. des Poissons, t. xviii, p. 245, Paris, 1846.

|| Duvernoy, Ann. des Sc. Nat., t. i, 3e, ser., p. 313, 1844.

¶ Agassiz, Am. Journ. of Science, xvi, 2d ser., Nov., 1853.

found only seven or eight fœtuses in the so-called uterus of each female, and each of the young was surrounded by a distinct sac, which he regards as simply an enlargement of the original envelope of the ovum. The mature fœtus he found to be more than one-fourth as long as the parent, and except for the non-development of the ovary was constituted in every respect like the adult, as regards both its internal and external structure.

"For the specimens of *Anableps Gronovii* upon which the following observations were made, I am indebted to the liberality of Dr. Francis W. Cragin, United States consul at Paramaribo, in Surinam. Among them were three males and five females, four of which last were in different stages of gestation. The different individuals varied from 3½ to 9½ inches in length, the females being much longer than the males.

"I. The smallest female measured 3½ inches in length, but on careful examination no traces of an ovary were discovered; its development did not appear to have commenced as yet.

"II. The next specimen measured 7 inches in length and the ovary was in a state of gestation; the fœtuses, four or five in number, measured but five-eighths of an inch. The ovary appeared single externally; was invested with peritoneum, which was supported by a more firm but thin membrane of condensed areolar tissue; on cutting through this the interior was found filled with sacs corresponding in number to the fœtuses and united to each other and the ovarian walls by a very loose areolar tissue. They had no communication of any kind with each other. With the aid of the point of a needle the sacs were easily detached and removed entire with the inclosed fœtus; the envelope was much larger than was necessary to hold the embryo, and the space between the two was filled with a fluid, a portion of which (albumen?) had been coagulated by the action of the alcohol. In each instance it was ascertained that the young had no connection whatever, vascular or otherwise, with the walls of the sac which inclosed it.

"The external characters of the embryo even at this early stage, as regards its general form and the fins, resemble those of the adult; but no longitudinal black bands were yet visible on the sides; the eye had not acquired the prominence of that of the adult, the cornea was not divided by a transverse band, and the pupil existed in the form of an oval, with its long diameter in a vertical direction, but the sides of the iris had just commenced extending towards the center in order to form the two laminæ, which in the adult give the pupil its singular shape. The umbilical sac forms a spheroidal mass about one-fourth of an inch in diameter, and is sufficiently transparent to allow the folds of the intestine which fill it to be visible. Externally the sac is covered with what appear to be parallel projecting lines, extending from the sides of the abdomen to its most prominent part. These Valenciennes describes as 'vascular striæ' (*stries vasculiformes*).* Such was not the nature of

* *Op. cit.*, ex fol. de planche, 539.

these markings in the specimens which I examined; but, when placed under the microscope, were found to form a peculiar structure, which possibly may have some connection with the process of nutrition in their peculiar mode of gestation.

"The sac itself seemed nearly homogeneous in structure, but the striæ are made up of spherical, or in some cases pyriform or cylindrical, papillæ or villi, projecting from the surface and arranged so nearly together in a linear series as to give the appearance of a continuous band. In regard to the minute structure of these papillæ, as far as it could be determined from an alcoholic specimen, they consist externally of an exceedingly thin membrane, inclosing a vast number of minute granules; no vessels were seen in connection with them nor in the membrane to which they were attached. There was no appearance of any communication between the cavity of the papilla and that of the membrane to which it was attached. Within the latter, but more nearly in contact with the intestines, there was a second more delicate membrane, which seemed to be a continuation of the parietal peritoneum. No traces of the yelk were found in connection with the intestines.

"III. The third specimen is much longer and measures 10 inches in length; the ovary had been ruptured, so that some of the fœtuses had escaped into the cavity of the abdomen, but the whole number of young taken from the parent was much greater than in the preceding case, namely, eighteen; one of these was projecting from the genital opening. They generally resembled the preceding except in size, though the eyes had become more prominent, and the iris now exhibited its lateral projections sufficiently developed to give the pupil the shape of a dumb-bell. The umbilical sac has become much larger than in the embryos first described, and measures three-eighths of an inch in diameter. The papillæ of the yelk-sac are much more distinct, and contain colored granules. The yelk-sac communicates with the cavity of the abdomen by a long fissure extending from a point just behind the union of the opercula nearly as far as the anal opening, consequently beyond the ventral fins. It is from the circumstance just mentioned, doubtless, that an explanation is to be found of the non-union of the ventrals in the adult. The scales terminate abruptly at the edge of the fissure. The intestine, as in the first described embryos, were invested by the internal sac, which was regarded as parietal peritoneum. No bands were visible on the flanks of the body, nor were the anal fins yet modified to mark the sexes. A rudimentary liver is visible in these specimens, extending backwards on the left side of the intestinal mass. The intestinal canal is of almost uniform size throughout, there being no distinction between intestine and stomach.

"IV. This specimen measured a little less than 10 inches in length, but the embryos were of much larger size, having a length of 2¼ inches; the umbilical sac had disappeared, but the fissure on the under side of the abdomen still remained, and, what seems quite remarkable, had grown in dimensions just in proportion to the entire fœtus, so that in

these specimens it measured 1 inch in length, and was consequently longer than the whole embryo of the first specimen noticed above. The edges of the fissure were united by the intermedium of a thin membrane, without scales, on which no papillæ were noticed, and was sufficiently lax to allow the edges of the fissure to separate from each other to a slight extent. The transverse band upon the cornea was now distinct, though it had not yet become as opaque as in the adult.

"Seven fœtuses were found in the ovary; on the sides of them one or two dark longitudinal l nes were now visible; the general form of the body had assumed more precisely that of the adult, and, as noticed by Valenciennes, the intestines had obtained their permanent form. The external sexual characters were not visible in any of the specimens examined, though they were seen and figured in specimens of about the same size by Valenciennes.

"All of the fœtuses of this female had escaped from their original sacs (no traces of which were now visible) and were all contained in one large cavity formed by the dilated ovary which now had become analogous to an uterus and extended from the genital opening as far forwards as the bases of the pectoral fins. The walls of this ovarian sac were sufficiently thin to allow the fœtuses to be seen through them. On its inner surface, as well as on that of some of the other specimens, were to be seen numerous immature ova, some of them microscopic and others as large as the sixteenth of an inch in diameter. The co-existence of immature ova on the walls of the ovarian cavity with fœtuses in it corresponds with what was noticed by Duvernoy in his investigations of the embryology of Pœcilia.* The more minute ovarian eggs, though for a long time macerated in alcohol, yet preserved their microscopic characters to a remarkable degree. The smallest consisted of a cell, in the center of which a nucleus was visible, and around this last were a few granules. In the larger ova the granules have become more and more abundant, and in some instances obscure the nucleus or germ-cell. After the egg has increased to a certain size, a clear space appears exterior to the vitelline membrane, which gradually increases to nearly twice the diameter of the egg itself. This clear space is limited by the substance of the stroma, which becomes condensed around it and thus forms a distinct sac. If the ovum be compared to that of a mammal, then the sac just described may be said to be analogous to a Graafian vesicle; that is, the egg of the fish floats free in a sac much larger than itself, just as the mammiferous egg does in the vesicle of De Graaf. There were no intermediate conditions between this and the impregnated condition to enable me to determine whether or not it is this sac which formed the external covering of the fœtus. Valenciennes seems to adopt the idea that it does, and compares it to a chorion.† If this view

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* Sur la developpement de la Pœcilia surinamensis, Ann. des Sci. Naturelles, 3e ser., i, p. 313, 1844.

† La cellule qui contient un oeuf fécondé s'aggrandit et finit par former une sorte de chorion. *Op. cit.*, t. xviii, p. 261.

of its nature be true, then there seems no alternative, since development advances so far before the sac ruptures, but to suppose that impregnation must take place through its parietes and that the spermatozöon cannot enter bodily into the substance or even come in direct contact with the vitelline membrane of the egg except through the walls of its outer covering, which is not probable. It would seem that it must act simply by its presence on the surface of the egg-sac or by an endosmosis of its fluid contents through the membranes by which the ovum is invested.*

"A microscopic examination of the egg-sacs in the advanced fœtuses proves conclusively that they do not consist of loose areolar tissue only, as stated by Valenciennes,† but that while the tissue in question forms the basis of them, they are in reality highly vascular, large trunks and minute ramifications of vessels being easily traced by the aid of the coagulated blood which they contain.

"In comparing fœtuses of different stages of development together, a very interesting question is presented to us in connection with their growth. In the smallest specimen examined, the yelk was no longer visible; it had been wholly consumed in supplying materials for the formation of the embryo; and yet subsequent to this disappearance of the yelk, the embryo, while still in its ovarian sac and cut off from all external communication, continues to increase in size, and grows until it acquires the length of an inch and a quarter, which gives the size of the longest fœtus which our specimens furnished. Even the umbilical sac and the fissure which succeeds it continue to grow after the yelk has disappeared. As a general rule among oviparous fishes, the yelk supplies *all* the material required for the growth of the fœtus; and the same holds good with regard to nearly all Batrachians,‡ to scaly reptiles and birds. So general has this rule been believed to be, that none but mammals have been supposed to contribute anything beyond the materials of the egg to the support of the young. But recent observations go to prove that some fishes, such as the Torpedo among the Plagiostomes, the Embiotoca among osseous fishes, are to be placed in the same category as mammals, in relation to the fact of being nourished by the parent during gestation, although neither a placenta is formed nor does any direct vascular communication whatever exist between the fœtus and the maternal circulation. We cannot explain the growth of the fœtal Anableps by any other hypothesis than that it is nourished by a fluid secreted by the walls of the sac in which it is lodged in the earlier stages, or by the parietes of the general ovarian cavity in which the fœtuses are received towards the end of gestation. The high degree of vascularity of the egg-sac is favorable to this supposition. As

[*See description below of the follicular pore in *Gambusia*.]

†*Op. cit.*, p. 261.

‡The only exception among Batrachians, as yet noticed, is found in the Pipæ of South America. See Observations on Pipa Americana, by Jeffries Wyman, M. D., in American Journal of Science, 2d series, vol. xvii, p. 369.

the body of the fœtus at a very early period becomes covered with scales, absorption could only take place through the intestinal canal or by the surface of the yelk-sac, which invests the viscera and increases in size for a long period after the yelk itself has wholly disappeared. In the later stages of gestation even the yelk-sac is out of the question, since it in turn wholly disappears, while the fœtus occupies the general cavity of the ovary."

Great interest attaches to the peculiar development of the rows of papillæ on the empty yelk-bag of *Anableps* as described above by Wyman. Its continued growth with the growth of the fœtus up to a certain stage of advancement is also remarkable; in fact, so far as yet known, it is unique amongst osseous fishes. The peculiar character of the villi on the yelk-bag remind one somewhat of what has been observed by Osborn in the structure of yelk-sac of the uterine fœtus of *Didelphys*, and by Owen in *Macropus*, in which the fœtal membranes fitted into uterine furrows, but were not adherent to the uterus and without villi. This structure in *Anableps* also reminds one of the hollow villi developed in certain mammalian blastodermic vesicles described by Bischoff. It is therefore unfortunate that Professor Wyman was not in a position to describe the minute histological structure of this abdominal sac in the fœtus of *Anableps* more fully, so that a more exact comparison could have been instituted between it and the yelk-bag or inferior pole of the blastodermic vesicle of the Marsupialia. A knowledge of the embryonic layers which enter into the formation of the yelk-bag of *Anableps* would also be a desideratum.

The extension downwards of the intestine of the embryo of *Anableps* into the empty yelk-bag is also interesting and reminds one somewhat of the peculiar protrusion of the hind-gut of Embiotocoid embryos into an inferior saccular diverticulum of the back part of the abdomen, which is obviously not homologous, however, with the globular, bag-like structure seen in the former.

Wyman does not state whether he examined the surfaces of the ovarian membranes in the earliest stages of development of the papilliferous sac to see if they did not present pits or crypts into which the papillæ may have fitted. These papillæ are obviously in some way connected either with the respiration of the fœtal *Anableps* or with its nutrition in the same way as are the marginal lobes of the fins of the fœtal Embiotocoids.

II.—The development of the Viviparous Surf-perches or Embiotocidæ of the Pacific coast.

Dr. Girard* states that the discovery that these fishes were viviparous was made in May, 1852, in San Diego Bay, California, by Dr. Thomas H. Webb, whose manuscript journal is quoted by Girard.

*Explorations and Surveys for a Railroad from the Mississippi River to the Pacific Ocean. IV. Fishes. 4to. Washington, 1858.

The following observations of his own have been put upon record in the latter's report, cited below; but it is evident that he overlooked the peculiar vascular lobes appended to the vertical fins of the embryos noticed by Blake, and also drew some erroneous inferences as to the identity of the yelk-sac, which will be noticed later. From pages 165 to 166, inclusive, of Girard's report the following paragraphs are quoted:

"But the most remarkable trait in the organization of the fishes of this family consist in the mode of reproduction. The eggs, instead of being laid, as is the case in most fishes, are retained within the body of the female, where they undergo not only their embryonic growth, but likewise a growth which might be termed larval, it being subsequent to their escaping from the egg envelope, until they have attained a size sometimes of several inches in total length. Nevertheless this peculiarity of habit is not altogether without analogy in the class of fishes. Moreover it bears no resemblance whatever to the marsupialian gestation; in the first place the eggs develop in the ovary, not in a uterus, and there is no placental connection of any sort; secondly, the young are not at liberty to quit and enter the ovarian cavities alternately and at pleasure.

"The observations which we have made upon the genital apparatus of the female have satisfied us that there exists an ovarian sheath or sac, which during the early period of pregnancy is an elongated and subcylindrical tube, containing the ovaries proper, two in number, each of which consist of two, three, or more vascular membranes, attached by their upper edges to the upper floor or roof of the sheath, forming either one or two pouches (according to the number of these membranes) of the same length as the sheath itself, widely open beneath, though not in direct communication with one another, since the membranes hang loosely down, reaching the lower floor of the sheath.

"The eggs are formed within the texture of the ovarian membranes themselves. We have examined the ovaries of *Ennichthys heermanni* and *Embiotoca argyrosoma* when the sheath within which they were contained was not larger than an ordinary quill. Numerous eggs could be observed in a very immature state, appearing to the unarmed eye like minute dots. Under the microscope they exhibited evident traces of the germinal vesicle, surrounded as yet with a very scanty supply of vitelline substance.

"The sheath and the ovaries are gradually increasing in bulk, as the eggs themselves first increase in size and the embryos afterwards. The sheath is chiefly a muscular membrane, while the ovaries, we have stated, are altogether vascular.

"When mature the eggs either fall into the space between the membranes or ovarian pouches, or else remain attached to the ovaries until the embryos issue out of them. We are inclined to think that they drop into the pouches as eggs. At any rate we found very young em-

bryos loosely contained in the ovarian pouches when no trace of the egg-membrane could be seen within the tissues of the ovaries in the shape of a *corpus luteum* or a Graafian vesicle. Whatever be the case, numerous eggs or embryos may be observed within one pouch. The young thus remain together until grown to a considerable size, when, filling up the space in a more compact manner, the ovarian membranes, in their nature very expansive, will extend a fold between each embryo. In this manner every individual young, when removed sideways from the ovary, appears to the operator as though inclosed in a separate cavity, pouch, or follicle of the ovary, whilst in reality the membranes may be stretched out or extended, and the entire progeny loosened from all adherence or connection with them.

"The male organs of generation consist of two spermaries, a right and a left, perfectly independent from one another, having each its separate duct, discharging their contents into an elongated cloaca, into which the bladder likewise empties its contents. This cloaca communicates with the exterior by a subcircular opening, the edge of which is rather protruding. Such is that apparatus, the same in its general structure as in the other osseous fishes. There is no sheath inclosing the two spermaries, and this fact throws considerable light upon the morphology of the ovaries; the latter being, in fact, two in number, but so closely connected together as to simulate a single organ. Thus the general disposition, not the plan of structure, of these organs is adapted to the mode of reproduction; a single sheath being a more simple adaptation than two, one for each ovary.

"How the mechanical act of fecundation takes place we are not prepared to say from direct observations; the eggs themselves must be fecundated within the ovarian sheath; a copulation of some sort is, therefore, required, and it is not improbable that at this period the eggs have dropped from the ovarian membranes into the pouches or spaces between these membranes in which they are freely floating."

Then follow some observations on the development of the embryos which are to a great extent erroneous, the "abdominal bag," alluded to as the yelk-sac, being probably the same as what I have determined to be the greatly hypertrophied hind-gut which protrudes from the ventral aspect of the body of the embryos. The cleft of the mouth, it is also stated, is not apparent at the time the fins began to grow out. This is also to be seriously doubted, and is a statement which probably rests upon defective observation, as I find the vent to be perforate at the time the embryos are an inch in length.

Farther on Dr. Girard, speaking of the embryos of *Ditrema jacksoni*, six to seven tenths of an inch long, "The yelk-bag was still to be observed in the shape of a hernia under the abdomen."

In *Embiotoca perspicabilis*, Girard states, *op. cit.*, page 179, that "a female on being opened was found to contain about eighty young of an average size of half an inch, the whole embryo consisting of cells

with no signs of the mouth. A layer of black pigmentum constituted the eye. Membranous ridges above and below showed the first steps in the formation of fins. The caudal itself was a mere membranous expansion of the cellular substance of the body. As such, the embryos had made their escape from the eggs."

Under *Phanerodon furcatus*, page 185, Girard again mistakes the protruding hind part of the intestine for a yelk-bag. On page 195, in embryos of *Holconotus rhodoterus*, from three-quarters to an inch in length, he speaks of this part of the intestine as "a vitelline abdominal sac."

An examination of the figures of the immature ovarian ova of Embiotocoids has served to convince me that those figured by Dr. Girard were very far from mature, and can give us but a slight conception of what they are like when ripe, because he represents the germinative vesicle as still central. The general rule that the nucleus breaks up and leads to the formation of a new nuclear center in an eccentric position in the egg will probably be found to hold in the Embiotocoids as in other fishes.* As Girard states, I find them embedded in the substance of the thick membranes which depend from the roof of the ovarian cavity.

The youngest fœtus figured by Girard is also pretty well advanced, all of the vertical fins being already defined. The comparison also of these youngest fœtuses hitherto figured with some somewhat older which I have had the opportunity to investigate, leads me to believe that the former were much farther advanced than was supposed by that author. His figures of the fœtuses are poor, and give a very imperfect idea of what it must actually have been possible to see. His statement that the mouth was still closed I am also inclined to doubt, while his observations on the development of the eye are simply calculated to force a smile. He has clearly mistaken the protruding and hypertrophied hind-gut in all of his figures for a yelk-bag, the latter having probably vanished long before, and at a point somewhat in advance of what he regards as the yelk.

III.—The hypertrophied hind-gut of Embiotocoid embryos and its subsequent diminution in relative size.

The hypertrophied hind-gut of Embiotocoid embryos which protudes into a sac-like downward projection of the abdominal profile is the most important of the embryonic visceral organs. Upon opening the abdominal cavity it is found that it fills up fully two-thirds of the latter, and that its dimensions, especially the transverse diameter of the gut, is far greater than the portion of the canal which subsequently becomes the stomach. Upon cutting this swollen hind-gut open its walls are found to be thickly clothed with crowded villi of the most extraordinary length, many being entangled together at their tips, and much

* See the law of nuclear displacement and its significance in embryology, Science, i, 1883, pp. 277, 278.

bent. If extended some of these villi would more than reach across the lumen of the intestine. This is their condition in the fœtuses of several species of Embiotocoids examined by me ranging from 1 to 1¼ inches in total length.

As development proceeds the gut begins to assume its normal dimensions posteriorly. It becomes narrower, and the sigmoid turn or flexures of the intestine more pronounced. The villi also diminish in length, and become far less numerous in fœtuses 1¾ inches long. At this stage, also, the projection of the rectum below the abdominal profile becomes less marked, and in fact is scarcely apparent.

In the adults the posterior part of the intestinal canal exhibits no such dilatation and dense internal garniture of villi as is seen in the fœtus; in fact, the hind-gut of the fully-grown fishes presents nothing unusual when compared with that of the usual type.

It is therefore obvious that this hypertrophy of the hind-gut and remarkable development of elongated villi in the embryos of the surf-perches has some important function to subserve during fœtal life. As suggested at another place, that function seems to be digestive; and as it is not at all improbable that the fluids secreted by the walls of the ovarian sac are nutritive; it seems likely that the fœtal fishes swallow such nutriment while still in the ovary. If Dr. Blake is correct in stating that the ovarian duct is occluded by a mucous or membranous plug during gestation, this interpretation of the function of the gut of the embryo would seem all the more likely to be the correct one.

IV.—The intra-ovarian respiratory function of the vertical fins of Embiotocoid fish embryos.

Two papers on the intra-ovarian gestation of the embryos of the *Embiotocidæ*, *Holconoti*, or surf-perches of the Pacific coast have been published by Dr. James Blake,* in the first of which the singular vascular lobes extending beyond the rays of the vertical fins, as productions of the inter-radial membranes, are for the first time described and figured.

I reproduce the following from Dr. Blake's second paper, as it will serve to indicate the extent of his contributions to the subject under consideration:

"The manner in which the young of the Embiotocoid fishes is nourished until it escapes from the ovary has not, that I am aware, been satisfactorily explained. In this class of fishes the young remain in the ovary until they are apparently as perfect as the adult fish. As during the process of gestation the ovary is cut off from all communication with the water, the external orifice being sealed up by a dense layer of epidermis or inspissated mucus, it is evident that the fœtal fish must

*1. On the nourishment of the fœtus in the Embiotocoid fishes. Proc. Calif. Acad. of Nat. Sci., iii, 1867, pp. 314–317, 3 figs. in text.

2. On the nourishment of the fœtus in Embiotocoid fishes. Journ. Anat. and Physiol. ii, 1868, pp. 280–282.

receive the elements of its growth from the interior of the ovary, and that it must be furnished with organs of absorption and respiration suited to the medium in which it is developed. A large supply of nourishment must evidently be required, as the ovary contains frequently forty or fifty young fish, which, when fully developed, measure more than 2 inches in length, and which together will weigh from one-twelfth to one-sixteenth as much as the parent fish. The ovary consists of a membranous bag partially divided at the upper (anterior) part, and terminating below in a narrow canal, which, in some species, opens externally in a cloaca common to it, and the urethra in others by a separate opening situated between the anus and urethra. The sac has three coats—a peritoneal, a muscular, and a mucous. The mucous layer is thrown into a number of longitudinal folds, and on the inner surface of the ovary the ova are found; and as the fœtal fish grows these folds extend so that each fœtus is in contact by each of two surfaces with the mucous membrane. The organ is well supplied with blood-vessels, an artery entering at each horn of the ovary. They arise from the aorta immediately after the union of the branchial arteries, and at the latter end of gestation each is larger than the descending aorta. The posterior part of the uterus (ovary) also receives vessels from the abdominal aorta. In the early stages of development the fœtus is embedded in a very tenacious secretion, which resembles para-albumen in that it can be drawn out into threads of a foot or 18 inches long. As gestation advances the secretion of the ovary becomes more fluid, and its quantity is increased so that as much as three drams can be obtained from one ovary towards the end of gestation. It then forms an opalescent fluid, specific gravity, 1.025; does not coagulate on heating; acetic acid throws down a white precipitate, mixed with equal parts of distilled water, and filtered, it has no action on polarized light; heated in an open vessel, a pellicle forms on the surface. It probably contains some albumen-compound, fat, salt, phosphates, and iron; but it has not been submitted to a careful analysis.* The fœtus during the earlier stages of its development goes through changes apparently analogous to those which take place in the ova of oviparous fishes, and it is not until the fins are formed that any departure from the ordinary plan shows itself. As soon as the fins were well formed the dorsal, caudal, and ventral (anal) fins became edged with a delicate membrane formed apparently entirely of capillary blood-vessels. As the fœtus grows this membrane is split up into processes or digitations, which extend a considerable distance beyond the margin of the fin, sometimes as much as a quarter of an inch. They retain the same structure during the whole period of development, and are so extremely

* This fluid is usually expelled from the ovary by the struggles of the fish when taken from the water, so that it is extremely rare to find one in our market in which the membrane closing the orifice of the ovary has not been ruptured. This is probably the reason that it has not been already noticed.

delicate that I have been unable to detect them in any specimens preserved in alcohol. As soon as the young fish is expelled from the ovary these processes rapidly diminish in size, and I have no doubt they entirely disappear after a few hours. Their use is evidently to absorb nourishment from the fluid in the ovary; they also serve to aerate the blood, for I have observed that on heating the fluid from the ovary, or on mixing it with ether, there is an abundant escape of gas. I think these facts serve to explain the manner in which the fœtus of the Embiotocoid fishes is nourished during its intra-ovarian development. They have been frequently observed in the three varieties of this sort of fish which are found in our waters."

Within a very recent period, through the kind offices of Miss Rosa Smith, of San Diego, Cal., I have been enabled to obtain some well-preserved material for purposes of study, which, while it enables me to add considerably to our knowledge of the development of these singular fishes, also impels me to differ to some extent from the conclusions of Dr. Blake. Miss Smith, at no little trouble to herself, obtained for me gravid females of *Amphistichus arenatus*, *Ditrema jacksoni*, and *Micrometrus aggregatus*. Unfortunately this material, as well as some in addition which I have obtained through the kindness of Dr. Bean from the collections of the National Museum, represents only the more advanced stages of fœtal development, so that I am unable to add anything to the very little which is known of the earliest stages of development. Judging from the dates upon which the specimens collected by Miss Smith were taken, it would seem probable that during the months of October and November one would probably find the earlier stages which are so desirable in order to clear up what must evidently be a most interesting chapter in vertebrate embryology.

The most striking characteristic of the fœtal surf-perches, as they lie in the ovarian sac of the parent fish, is the exaggerated development of the vertical or median fins, all of which combined present a lateral area almost or quite as great as the united areas of the side of the head, body, and tail. These fins present an exaggerated length and height nowhere approached by the adults, and not exceeded in respect to the width and relative length of the caudal fin by any fishes except perhaps some of the domesticated Japanese breeds of *Carassius*, such as the Kin-yi-ko. This extension of the area of the vertical fins is still further increased by the production of the interradial membrane into thin, highly vascular processes or marginal digitations. These Dr. Blake has already described, but he has not mentioned the very extraordinary way in which these structures acquire their blood-supply, which is, so far as I am aware, unique amongst young fishes, though faintly approximated by the arrangement of the blood-supply seen in the enormously developed translucent caudal of the Kin-yi-ko, as I have had the opportunity to observe in the living fish.

Description of the vascular supply of the vertical fins of Embiotocoid

embryos will be necessary before it is possible to comprehend the meaning and importance of the vascular digitations at the edges of those fins. All of them receive their blood-supply from the median aortic trunk.

The trunks given off to the dorsal fin traverse the median plane of the body and tail, and pass up in a nearly straight direction to the base of the dorsal, at irregular intervals of one, two, or even six muscular segments. Upon reaching the base of the fins they subdivide into from two to six branches, which pass up a little to one edge of the interradial space, but give off smaller trunks along their entire course through the interradial membrane, which is highly vascular. Continuing they proceed to the margin of the fin. They end in a flat sieve like capillary mesh, which fills up almost the whole of the marginal lobes formed by the prolonged interradial membranes. The tissue of the walls of the vessels within these terminal interradial lobes seems to be mesoblastic, but their external walls next the exterior seem to be mostly epidermic and exceedingly thin, probably not more than three or four cells thick. The capillary mesh is most complex and finest in the terminal lobes, less so in the interradial spaces.

The digitations on the spinous portion of the dorsal are very feebly developed, in fact scarcely apparent between the tips of the nine spines of the spinous part of the dorsal of a fœtus of *Micrometrus aggregatus*, a species in which these spines develop, by the way, in a continuous fold, and not in separate pockets or diverticula as in *Lophius* and *Gasterosteus.* * Four principal vessels supply the interradial and terminal capillary meshes of the soft dorsal with blood. These four vessels pass in an almost vertical direction from the aorta to the base of the fin, and do not follow the curvatures of the intermuscular septa. No vessels of unusual caliber pass to the spinous part of the dorsal.

The terminal or marginal interradial lobes of the anal of the fœtus of *Micrometrus* are twenty-six in number, or three in excess of the dorsal, while the two spaces between the anterior spines of the anal are without produced vascular lobes. Five principal vascular trunks pass vertically downward to the base of the anal, where they subdivide and supply each of the interradial spaces. The marginal lobes of the anal and dorsal are about alike in length and all have a marginal vessel circumscribing the capillary mesh at their edges. In this last respect they are like the terminal lobes of the caudal, in which they are, however, somewhat larger and longer.

From what has been said above it will be noticed by the reader that the number of vascular trunks passing outward to the bases of the vertical fins does not correspond to the number of rays which they contain. This fact indicates that this singular vascular supply of the vertical fins of Embiotocoid embryos has attained great specialization and must be of very great physiological importance.

This fact is rendered still more striking when we come to consider the vascular supply of the caudal fin, which is quite unique so far as I

* See Am. Naturalist, 1885, p. 415.

am aware amongst existing fish embryos. In the caudal, the posterior extremity of the aorta is prolonged backward, slightly bent upward, to beyond the anterior ends of the rays where it divides into two branches, a ventral and a dorsal one, each running nearly vertical to the axis of the body along the base of the caudal. From their posterior sides these two branches each give off about eleven or twelve secondary twigs which run out along and between the rays through the interradial spaces to supply the capillary mesh-work of the latter and the terminal lobes.

The membranous fold which is continued forward dorsally and ventrally from the base of the caudal, and which is a remnant of the continuous median fin-fold of an earlier stage, is also very vascular, but gets its blood supply from vessels arising from the aorta in front of the caudal. The foregoing is the arrangement of the vascular system of the fins in fœtuses about 1 inch in length. On comparing this stage of *Micrometrus* with *Amphistichus* 1½ inches long, it was observed that the vascular apparatus above described had already begun to diminish in importance, and in the adults nothing could be found which exactly represented it. The conclusion, therefore, is that like the vessels which render the skin of the fœtal Embiotocoid so highly vascular, this system atrophies for the most part after having temporarily subserved some important function.

The skin of the fœtal *Micrometrus* was highly vascular, and it was observed that special trunks passed outwards to the skin along the sides, these vessels arising for the most part above the aorta from the sides of the vessels which passed to the dorsal and the muscles of the tail. The vascular network beneath the skin is remarkably well defined and could obviously not be for the purpose of supplying the skin alone with blood.

The complex and unique vascular apparatus of the vertical fins of Embiotocoid fish embryos it seems to me to be mainly for the purpose of effecting respiration through the skin, and not for the purpose of absorbing nutriment from the ovarian space as Dr. Blake, has supposed. My reason for entertaining such an opinion is the fact that the mouth of the fœtus is now open and that the throat is perforate, and that the back part of the intestinal canal is widened and clothed internally with extraordinarily long and densely crowded villi. In fact this part of the intestine has been hypertrophied in the fœtus, and while there was no food found by me in the alimentary canal, I cannot but believe that this part of the intestine is already functional and subserves all of the purposes of the alimentary apparatus of the adult, and that the albuminous substances secreted in the ovarian cavity are swallowed by the fœtus, and finally digested by the peculiarly organized hind-gut which I have described. There is, therefore, it seems to me, nothing left to do for the produced vascular membranes of the fins and the skin except to aid the gills in respiration, the interchange of gases between the parent and the fœtus taking place through the fluids contained in the ovarian cavity, and in much the same manner as in *Gambusia*. The

structure of the median fins of these embryos is such that, while their marginal lobes somewhat resemble the fœtal villi of the mammalian placenta, they differ from the latter in not being received into maternal crypts, which I diligently but vainly sought for on the surface of the folds which depend from the dorsal wall of the ovary.

The vascular net-work of the ovary by which the maternal blood is brought into indirect contact with the marginal lobes of the vertical fins of the fœtuses is derived from a strongly-developed pair of vessels which enter the two anterior coruna of the ovarian sac. These give off branches to the dorsal, thickened wall of the sac and others to the pendent membranes which extend downwards from its roof, between which the advanced fœtuses are packed in a somewhat irregular manner.

V.—The development and intrafollicular gestation of Gambusia patruelis.

During a temporary residence at Cherrystone, Va., in August, 1881, my attention was directed by Col. M. McDonald to the existence of a small Cyprinodont in the fresh-water streams of the vicinity. The females were gravid, the ovaries of most consisting of twenty to twenty-five yellowish eggs about one-twelfth of an inch in diameter. This species, which proved to be *Gambusia patruelis* of Baird and Girard, does not, as do most other fishes, commit its ova to the care of the element in which it lives, but carries them about in the ovary, as do most of the members of this family, where they are impregnated and where they develop in a very remarkable manner.

Of the manner of impregnation of the female we know very little except from the observations of Mr. Duly, who has related to me what he has noticed in the actions of the adults kept in aquaria in the National Museum. I have appended Mr. Duly's observations at the end of this paper.

In the adult male, which measures 1⅛ of an inch in length, the anal fin is strangely modified into an intromittent organ for the conveyance of the milt into the ovary of the female; a tubular organ appears to be formed by three of the foremost anal rays, which are greatly prolonged and united by a membrane. At the apex these rays are somewhat curved toward each other, and thus form a blunt point, but the foremost one of the three rays is armed for its whole length with transverse ridges, and with sharp recurved hooks at its tip, the other two at their tips similarly with hooks, and between their tips are two small fenestra or openings which possibly communicate directly with the sperm duct from the testes. The basal interspinous bones of the anal fin are bound together by fibrous tissue into a cylindrical columnar bony mass, truncated above, and is prolonged upwards from the inferior abdominal parietes behind the anus into the cavity of the air-bladder for the distance of nearly the eighth of an inch; from the upper truncated end and the posterior side of this column a series of fibrous

bands pass to the dorsal and posterior wall of the air-bladder, to be inserted in the median line. Whether this bony column serves to steady the fin in the act of copulation, or whether it serves to give passage to the sperm duct are unsettled questions with the writer. The modified, almost styliform, anal fin of the male measures a third of an inch in length, or nearly one-third of the total length of the fish.* Other peculiarities of the male are noticeable, for instance, the more abbreviated air-bladder, which also occupies a more oblique position than in the female. The most remarkable difference presented by the male as compared with the female, however, is his inconsiderable weight, which is only 160 milligrams, while that of the gravid female is 1,030 milligrams, or nearly six and one-half times the weight of the male, an unusual difference in the relative sizes of the two sexes amongst fishes.

The adult female, as already stated, is heavier than the male, and measures $1\frac{3}{4}$ inches in length. The liver lies for the most part on the left side. The intestine makes one complete coil or sigmoid flexure upon itself in the anterior half of the body-cavity; its posterior third passes back along the floor of the abdominal cavity, and at the posterior end of the latter the Wolffian ducts traverse it vertically, to be enlarged near their outlets into a fusiform urinary bladder.

The ovary is a simple, unpaired organ, the greater part of which lies on the right side of the body-cavity below the air-bladder, and serves to fill up the greater part of the inferior moiety of the former when developed to maturity with its follicles gravid with embryos. The ova, when full grown, are each enveloped in a sack or follicle supplied with blood from a median vascular trunk, which divides and subdivides as it traverses the ovary lengthwise in a manner similar to that of the stem to which grapes in the bunch are attached. The arrangement of the ova and their attachment to the median vascular rachis is well shown in Fig. 11, Plate VIII, in which the immature ovarian eggs are also represented as small whitish bodies attached to the sides of the vessels. In Fig. 10, Plate VIII, two of these immature ovarian ova are also shown close to the *follicular pore* of a follicle containing an advanced fœtus.

Every fully-grown ovum, by means of the preceding arrangement, has its own independent supply of blood from the arterial system of the mother, the ovarian arterial trunk being a branch of the median dorsal aorta. Each egg and egg-sac is thus supplied with materials for its growth and maturation, the latter eventually becoming specialized into a contrivance by which the lives of the developing embryos are maintained while undergoing development in their respective follicles. The young or unripe eggs which are found together in the same ovary with the developing fœtuses are, as stated above, enveloped in a cellular and fibrous stroma, which serves not only to strengthen the vessels, but

*The anal fins of the males of closely allied species of *Gambusia* and of *Limia*, from Cuba, are similarly modified, according to Prof. Felipe Poey, who has figured those observed by him in his Memorias sobra la Hist. Nat. de la Isla de Cuba, i, pp. 382–387, pls. 31 and 32. Habana, 1851.

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also afterwards enters into the structure of the walls of the ovarian sacs or follicles externally, as these grow in size.

The immature ova measure from a hundredth to a fiftieth of an inch, and enlarge to something more than a line in diameter, when they may be said to be mature. The median vessel of the ovary extends backward and slightly downward, and arises very far forward in the roof of the body-cavity from the dorsal aorta.

The ova after developing a little way are each inclosed in a follicle or ovisac, *membrana granulosa* of Von Baer, or *membrana cellulosa* of Coste. As the egg develops there seems to be a space gradually formed about it in the same way as described by Wyman in *Anableps*. This space is filled with fluid, and in this liquid, which increases in quantity somewhat as development proceeds, the embryo Cyprinodont is constantly bathed.

There is no trace whatever in the egg follicles of Gambusia of an independent egg membrane, such as is present in the ova of all known forms of osseous fishes which spawn directly into the water, the egg membrane or *zona radiata* of the latter, in all cases being perforated by a minute pore or micropyle for the passage of the spermatozoa. The condition in *Gambusia* raises the question whether the *zona* is not more or less completely aborted, sooner or later, in all viviparous fishes. Wyman, however, points out that a membrane exists, covering the immature ovarian eggs of *Anableps*, and I find that the mature eggs of *Fundulus* are provided with a strong zona radiata during the early stages of their intra-ovarian development; how long it persists, however, has not been determined, as it is possible that it is disintegrated and absorbed during the later stages of gestation. Rathké's description of the ovarian follicles of *Zoarces* agree in some respects pretty closely with my account of the egg-follicles of *Gambusia* given farther on. The narrow elongate stigma, devoid of vessels, on the follicle, spoken of on page 4 of his memoir on Zoarces, probably corresponds to what I have called the *follicular pore*. He has described a vascular net-work in the follicle, a stalk joining it to the vascular rachis, and a space around the yelk much as in *Gambusia*.

The zona radiata, or covering of the eggs of osseous fishes, is said to be secreted from the cells lining the follicles, and is composed of a strong, somewhat gelatinoid substance, and is usually, though not always, perforated all over by a vast number of extremely fine tubules, called *pore canals* by their discoverer, Johannes Mueller. In the yellow perch (*Perca flavescens*), the zona radiata is well marked, but external to it there is a highly elastic layer many times thicker, which is traversed by what seem to be tubules, which are, however, much less numerous than those of the true zona. In the ova of closely allied forms, such as the white perch and r ck-fish or striped bass, this extra external envel-

ope is wanting. In the ova of the Ganoids, *Amia* and *Lepidosteus*, the *zona* is composed, in the first instance, at least, of short, parallel, elastic fibers disposed in a plane vertical to that of the membrane, these fibers being fused at their ends or just below the inner and outer surfaces of the membrane. Sections through the egg membrane of *Lepidosteus* seem to indicate the same condition of things as in *Amia*, in fact, Dr. E. L. Mark, of Cambridge, Mass., has kindly shown me drawings which show the fibers of the zona of the former isolated in the same condition as I have been able to separate those forming the egg-membrane of the latter.

The egg-cases of the oviparous Plagiostomes have a different structure from the zona investing the ova of osseous fishes in that they are fibrous in structure and of a horny consistency, the fibers running in a direction parallel with the surfaces of the case. The ovoviviparous forms, judging from the character of the egg-cases of *Squalus*, have the walls of the case extremely thin, apparently to facilitate the interchange of the gases needful in fœtal respiration during development in the oviducts.

The skate's eggs have two hollow processes at each end of the peculiarly formed case, which are perforated at the sides and which afford passage for the water in and out of the case needful for the respiration of the developing embryo. The egg-case of *Heterodontus* or *Gyropleurodus*, a specimen of which has been sent me by Miss Rosa Smith, may be compared to a skate's egg, which is narrower at one end than at the other, but which has been molded into a spiral form during its formation in the oviduct, and which has traces at either end of openings which are apparently homologous with those found in the latter.

The preceding data render it evident that there is a wide range of variation in the character of the investments which cover the ova of different species of fishes, and it is obvious that, while all of the various forms are for the purpose of giving protection to the ovum, some of them are modified to minister to the respiration of the embryo. In other cases a modification of the membrane such as exists in the adherent ova of *Amiurus*, may have still another function to subserve, viz, that of enabling the male parent to aerate the eggs without injury during his apparently violent movements over them with his anal and ventral fins. In *Amiurus* a double membrane invests the egg; an outer highly elastic one separated from the inner or true zona by a shallow space filled with water, but attached to the latter by irregularly disposed elastic pillars of the same material as the outer envelope. The outer envelope is also very adhesive, so that the masses of ova in their elastic investments may be repeatedly moved about or shaken up by the old fish without injury or risk of detachment.

The variability of the egg-membranes of the class *Pisces*, as restricted by Jordan, is rendered still more striking when the types with filamentous appendages, such as *Menidia*, *Belone*, *Exocœtus*, and *Gobius*, are considered. No trace of such a structure existing as a covering for the

egg of *Gambusia*, we are in a position to ask the question why such an unique condition of affairs should exist in this case. The answer, it would appear, we need not go far to seek. In the case of eggs which ordinarily hatch in the water it is necessary that they should be supplied with a covering more or less firm and capable of protecting the contained embryo, which, in the case of *Gambusia*, is not needed, because the embryo is developed so as to be quite competent to take care of itself as a very well organized little fish when it leaves the body of its parent. Nature will not waste her powers in an effort to make useless clothes for such of her children as do not need them; on the contrary, she is constantly utilizing structures economically, and often so as to serve more than one purpose at one and the same time.

The ovarian follicles of *Gambusia* containing mature ova or fœtuses are built up internally of flat or squamous polygonal cells of pavement epithelium, and externally of a net-work of multipolar, fibrous connective tissue cells and minute capillary blood-vessels with cellular walls, which radiate in all directions over the follicle. From the point where the main arterial vessel enters it, this vessel, together with its accompanying vein and investment of fibrous tissue, constitutes the stalk by which the follicle and its contained naked ovum is suspended to the main arterial trunk and vein. The minute structure of the follicular membrane is shown in Fig. 14, Plate IX; the capillary system of the follicles converges by way of the veinules which join the large median ovarian vein which follows alongside the course of the ovarian artery back to the heart. The very intricate mesh-work of fine vessels which covers the follicle supplies the developing fœtus with fresh oxygen, and also serves to carry off the carbonic dioxide in much the same way as the placenta or after-birth performs a similar duty for the young mammal developing in the uterus of its parent. There is this difference, however, between the fœtal fish and the fœtal mammal: In the former there is no uterus; the development takes place in the follicle in which the eggs have grown and matured; there is no placenta, but respiration is effected by a follicular mesh-work of blood-vessels, and the interchange of oxygen and carbonic dioxide takes place through the intermediation at first of the fluid by which the embryo is surrounded in its follicle, and later, when blood-vessels and gills have developed in the embryo (see Fig. 17, Plate IX), they, too, become accessories to aid in the oxygenation of the blood of the fœtus.

In the mammal, on the other hand, there is a uterus; the egg must leave its ovarian follicle; be conveyed to the uterine cavity before a perfectly normal development can begin; there is a fully developed, richly vascular placenta joined to the fœtus, the villi or vascular loops of which are insinuated between those developed on the maternal surface of the uterine cavity. In both fish and mammal, however, the following general likeness remains, viz, that there is no immediate vascular connection between mother and embryo. In both the respiration of the embryo is effected by the transpiration of gases through the intermediation of

membranes and fluids, oxygen being constantly supplied and carbonic dioxide carried off by means of a specialized portion of the blood-system of the maternal organism.

There is still another character which distinguishes the development of *Gambusia* from that of the mammal. The body of the former is built up by a gradual transformation or conversion of the substance of the yelk into the various structures which make up its organization. In other words, the young *Gambusia* obtains no nutrition from its parent; there is merely an incorporation by the embryo of the stored protoplasm of the yelk-sac. In the Eutherian mammal, on the other hand, hand, the embryo receives nourishment through the placental apparatus; by far the greatest proportion of the embryo being built up from the protoplasm supplied and conveyed to it from the blood-system of the parent. Judging from the large size of the young of some viviparous fishes, such as those of *Anableps* and the *Embiotocidæ*, it is obvious that there are exceptions to the method of development characteristic of *Gambusia*.

Besides the very intricate net-work of capillary vessels which covers the follicles of the ovary of *Gambusia*, a large opening, Figs. 9, 10, 11, and 12 *mp*, Plate VIII, and Fig. 13, Plate IX, of a circular, though usually more or less oval, form makes its appearance in the wall of each one at or near the point of attachment of the vascular stalk by which they are supported. This opening appears to increase in size as the young fish develops; whether it is present during the earliest stages of the intrafollicular development of the embryo I do not know, as I did not have an opportunity to see those phases. A branch from the main nutritive vessel frequently lies near the margin of the opening, curving around it. Whether this opening serves the same purpose as the micropyle of ova provided with a membrane would appear very probable, as it is difficult to see in what other manner the milt, which is probably introduced into the abdominal cavity by the male, could reach the ovum through the wall of its follicle. The ovary itself seems to have no exterior investment, so that the follicles lie directly within the abdominal cavity, the young fishes upon the completion of their development rupture them and escape into the latter, and from thence through an abdominal pore into the outer world. The opening into the follicle licle may be named the *follicular pore*. Through it the cavity in which the embryo lies is brought in direct communication with the cavity of the abdomen, because it is extremely doubtful if the ovary as a whole is invested by a distinct membrane. If it is, its tenuity is extreme, since the follicles when gravid are readily separable as if entirely uncovered, or as if there were no external peritoneal investment reflected over them.

The nearly globular vitellus of the mature egg measures about a line in diameter. The germinal protoplasm probably occupies a peripheral position covering the nutritive or vitelline portion of the egg as a continuous envelope with strands of germinal matter running from it down

through the yelk substance. At the time of fertilization it is probable that the germinal matter is aggregated at one pole of the yelk. The latter in *Gambusia* is orange colored, and embedded between it and in the periblast superficially are a great number of refringent oil globules of small size.

The body of the young fish lies in a groove or furrow on the surface of the yelk at about the time the tail is beginning to bud out, as shown in Fig. 13, Plate IX, which represents the youngest stage of *Gambusia* which I have been able to observe. The somites or segments of muscle plates had been developed for some time, and the heart, brain, intestine, and organs of sense were well defined.

The next stage observed was that represented in Fig. 1, Plate VI, figured from the fresh embryo removed from its follicle.

The mouth is not yet well open and the pericardiac cavity seems to have its anterior or inferior wall supported by the end of the snout. The heart lies on the floor of this cavity on the yelk, with its venous end directed downward and forward. The vitelline net-work of vessels arise behind from the caudal vein, which bends down when it reaches the yelk, when it divides and sends a trunk forward along either side of the latter to join the rudimentary Cuvierian duct which runs down upon the yelk in the vicinity of the liver where the portal vein anastomoses with the latter.

The air bladder *ab*, Fig. 1, does not yet fill up the peritoneal cavity *pp*, and the liver *L* is quite large and lies on the left side. The intestine is not yet much bent or coiled upon itself.

The auditory vesicle and otoliths are well defined, and the eye and top of the head are pretty well pigmented.

The lateral line organs, or the *neuromasts* of R. Ramsay Wright, are present at this stage over each muscular segment, as shown by the small circles *nh* of Fig. 1. But at a later stage similar organs are found at the anterior border of the opercles, lodged in depressions of the skin as shown in section much enlarged in Fig. 20. These last-mentioned terminal sensory disks or *neuromasts* in the skin over the cheeks appear to derive their nerve supply from the great fifth pair.

The fins at this stage consist of the pectoral, dorsal, anal, and caudal; the ventral is not yet developed. Rays have commenced to form in the caudal; the others do not yet present any well-marked indications of rays, which only become well defined during the later stages shown in Figs. 2 and 3, when the ventral first appears as a papilliform rudiment on either side a little in front of the vent. No sexual differentiation of the anal fin was observed in any of the embryos taken from the follicles, and it is therefore inferred that such differentiation occurs during post-fœtal life.

The next stage observed is that represented in Fig. 2, which is drawn from a specimen hardened in chromic acid, and is consequently a surface view. The striking peculiarity which this specimen renders apparent is the prolongation upwards and forwards of a process of

the yelk-bag over the opercles at *py*. In other hardened specimens this pouch was observed to be prolonged upwards so as actually to meet its fellow of the opposite on the top of the head. In this way it happens that a sort of girdle is formed by the hollow cornua arising from the sides of the yelk-sac, which thus surround the head.

The next stage, Fig. 3, is from a living fœtus liberated from its follicle. In this specimen the scales were already developed, though the yelk was not yet absorbed, but was considerably diminished in amount. The heart still had its venous end directed downwards, gathering the blood from the net-work of superficial vitelline capillaries through a great median ventral vein, the same as in Fig. 1. In a cross-section, Fig. 15, from a specimen a little more advanced than that represented in Fig. 3, the dermal pouches in which the scales are developed are shown at *sp;* the section has also cut through the more advanced ventral at *vt* and the anal at *a*.

A remarkable characteristic of the embryos of *Gambusia* is to be noted in the fact that they do not develop continuous fin-folds, but, as shown in Figs. 1, 2, and 3, the vertical fins at once appear as distinct folds. This type is therefore not perfectly lophocercal or provided with a continuous eradiate dorso-ventral fin-fold such as is found in the embryos of *Gadus* of the same relative stage of development.

Chondrocranium.—The cartilaginous skull of *Gambusia* at about the stage represented in Fig. 3 is shown in detail in Fig. 21, Plate X. The brain-box has an incomplete roof; there is a cartilaginous bridge over the pineal region *T cr*, and one over the medulla oblangata *oc*. On its floor there is wide pituitary interval, as seen in Figs. 21 and 28, into which the hypophysis *Hy*, the infundibulum *In*, and optic nerve II, and crus *ch* project downward more or less decidedly. The chorda projects a considerable distance under the hind-brain, as may be inferred from Fig. 16, representing a longitudinal section of its anterior end, the vertebræ *vr*, *vr* being already differentiated with their intervertebral ligaments *l*, *l*, defined.

The auditory vesicle *Au* is covered externally by cartilage, and the orbit is limited above by an imperfect supraorbital curved cartilaginous bar, below by the pterygopalatine and hyomandibular bars. The nasal fossæ are limited behind by the cartilaginous orbito-nasal septum, below by the rostrum. The hyomandibular *Hm* is remarkably long and slender when embraced together with the symplectic *Sy*. Meckel's cartilage, *Mk*, is short; the glosso-hyal *G. Hy* is long; the hypo-hyal, *Hy*, nearly globular; the cerato-hyal, *C. hy*, wide and somewhat prolonged and joined to the hyomandibular by a short interhyal, *IH*. The branchiosteges *Brs* originate in perichondrial membrane, and have no cartilaginous rudiments. There are five branchial arches, I, II, III, IV, V, and detached suprabranchial nodules, *S. br*.

Behind the branchial arches, but more superficially, lies the cartilaginous coraco-scapular rudiment *Cor*, *Sc*, with the cartilaginous plate from which the actinosts are formed, abutting against it posteriorly.

The posterior branchial arches support clusters of teeth, which, in the sections studied by the writer, presented the forms represented in Figs. 26 and 27. A saccular organ, *df*, was developed from the deeper layer of the epidermis, in which the conical crown of the tooth, *d*, is first formed, as shown in Fig. 26, but with the progress of development the perichondrium *pch*, Fig. 27, which invests the cartilaginous branchial bar *Br*, forms a basal cushion, *s*, *s*, *s*, for each tooth, the conical crowns *d*, *d*, *d* being evidently articulated to the summits of these cushions, which give rise to the so-called cementum plates. It would thus appear that the crowns of the pharyngeal teeth, like the dermal denticles of certain forms, arose separately from the basal parts, which it is very clear develop later than the crowns in this instance, in intimate relation to the perichondrium investing the branchial bar, and therefore have a deeper origin than the crowns. The saccular organ, *df*, is developed from a more or less nearly solid diverticulum of the deep layer of the epidermis, which, in some cases, finally loses its connection with the latter, and becomes hollowed out inferiorly into a cap-like organ in which the germ of the crown appears.

The branchial filaments in the advanced embryo shown in Fig. 3 already have cartilaginous axes, *c*, as shown in Fig. 17; the base of the axis of the filament being furcate, and resting astride of the branchial vein *vb*, and not quite in contact with the branchial arch *bh* itself. These filaments are already pinnate and vascular.

The vertebral column.—The anterior part of this organ has already been described. The vertebræ are best differentiated anteriorly; in the tail the membrane in which the ossification of the centra occurs is apparent but not so strongly marked as anteriorly. The chorda bends upward but slightly at its hinder end, so that the urostyle is finally very short, as shown in Fig. 18.

The ribs are developed in cartilage as a single line of longitudinally compressed cells, as shown in Figs. 19 and 23 at *rb*. In the anterior thoracic region the heads of the ribs are elevated above the level of the chorda and are embedded in the fibro-cartilaginous rudiments *sk* of the neural arches, as shown in Fig. 23; posteriorly the ribs have their heads lowered more and more and assume a more ventral and intimate relation to the skeletogenous sheath of the chorda.

The fin-rays of the caudal fin in the most advanced fœtuses are already pretty well developed in membrane, beneath the epidermis; their relations to the mesoblast *me* internally and externally to the malpighian layer *sl* and epilthelium *ep* being shown in the cross-section represented in part in Fig. 24, and in Fig. 9 at *t*.

Visceral anatomy.—The way in which the fœtus is coiled up in the follicle is shown in Fig. 4, in which the process of the yelk-bag *py*, which extends upward over the opercles and to the top of the head, is also shown. In Fig. 9 a section through a follicle with the embryo in place and cut through at three different points is shown. This section also shows the open follicular pore *mp* with a thickened margin and the fol-

licular artery *fv* at the outer border of the thickened edge of the membrane.

The yelk *y*, liver *l*, intestine *i. i, i*, the air-bladder *ab*, the Wolffian ducts *Wd*, *Wd*, the aorta *ao*, chorda *ch*, muscles of the pectoral *pf*, &c., are also shown in Fig. 9. But in order to comprehend the visceral anatomy of the fœtal stages of *Gambusia*, Figs. 5, 6, 7, 23, and 25 are more satisfactory.

These sections will render it obvious once for all that in this form at least there is no connection whatever of the yelk with the intestine. That there is a wide space, *sc*, between the intestine posteriorly and the vitellus *y* is plainly shown in Figs. 5, 6, and 7.

The yelk also presents a well-marked periblastic layer, *yh*, in which the oil globules are embedded superficially. This periblastic stratum is thickest on the outer surface of the yelk and in the vicinity of vessels, but quite thin where it forms the floor of the abdominal cavity. In the cross-section, Fig. 5, the periblast sends up a median septum which divides the cruder yelk or deutoplasm into two moieties. Superficially the periblast has the vitelline vessels impressed into its surface, and in consequence of the fact that I have been unable to find a distinct cellular wall on their inner or periblastic sides I infer that the yelk is taken up from the periblast directly by the vessels. The cleavage cavity is persistent as in other Teleosts, and is apparent on either side of the vitellus in Fig. 9.

The heart, the details of which are shown in transverse section in Fig. 8, extends down into the anterior end of the yelk-sac, as shown in Figs. 6 and 7, having been first extended into the cleavage cavity, as indicated in Fig. 13. The most inferior chambers of the heart receive the venous blood. and all are thin walled except the ventricle *ve* and the bulbus aortæ *ba*, Fig. 6. The heart, as well as the liver and intestine, is more or less impressed into the surface of the yelk.

The œsophagus is somewhat bent upward posteriorly, from which extremity the air-bladder arises somewhat to one side. The pneumatic duct is open in the fœtus and is short, leading abruptly into the air-bladder *ab*, which is a depressed sac, the floor of which is very much thicker than the roof. The liver is a very massive organ relatively, and opens into the alimentary canal in the vicinity of its first turn. A large portal vessel passes from the liver outwards to the left, as shown in Fig. 5, and communicates with the vitelline system of vessels. What seems to represent a pancreas is seen in some sections adherent to the intestine, as shown in Fig. 6. In the posterior and upper part of the abdominal cavity, behind the intestinal coil, are placed the reproductive organs *o*, as indicated in Figs. 6 and 7; with greater magnification of that part of a cross-section the reproductive organ or genital folds have the appearance indicated at *o* in Fig. 25, which shows the organ in its indifferent stage, when it is quite impossible to tell whether the large nucleated cells embedded in it are going to give rise to ova or to spermatozoa. They lie on either side of the mesenteric suspensor of the intes-

tine; are, in fact, thickened ridge-like swellings of the sides of the mesentery.

The renal system lies almost wholly exterior to the abdominal peritoneum of the embryo, and is the only organ, with the partial exception of the air-bladder, which does so. The renal or Wolffian organ of *Gambusia* consists of a remarkably well-developed anterior mesonephric portion *pn*, Fig. 7, which is crowded up against the auditory vesicle posteriorly and richly supplied with blood-vessels. The pronephros was not observed, as the stages studied by me were already too far advanced, but the posterior part of the segmental duct was still essentially pronephric in character, as no segmental tubules opened into it. At the hinder aspect of the urinary vesicle *al* the segmental duct of the one side joined its fellow of the opposite side, and shortly after opens into the bladder, which has a distinct outlet, which lies in a line continuous with that of the segmental tubes when the latter are viewed from the side. In Fig. 23, *Pn*, a cross-section of the anterior mesonephric organ of *Gambusia* is shown, and in Fig. 25 the segmental or Wolffian ducts *Wd.* are shown in cross section through the region of the posterior part of the abdomen.

The brain.—A vertical longitudinal section of the brain of a fœtus of *Gambusia*, which has attained about the development of the one shown in Fig. 3, is shown in Fig. 28. The cerebellum *cer* is unusually wide antero-posteriorly, resembling in this respect the cerebellum of *Amiurus* of about the same age. The oral epithelium is shown in place at *oep*, and at *Hi* there is an involution which seems to represent the last vestige of the hypophysial pouch from which the hypophysis *Hy* has been developed, and from which that structure has become disconnected.

The *muscular system* presents nothing essentially different from that to be met with in other fish embryos. The so-called lateral dermal muscle *Dm*, Fig. 23, is distinguishable as a distinct layer of fibers external to the myotomes *m*, *m*, *m*, but it is remarkable that this muscle still shows the segmented condition seen in the latter, a feature which it does not share in common with the dermal muscles of higher animals. It is therefore seriously to be doubted if it has any very strong claim to be called a dermal muscle.

The courses of the fibers of the muscles of the body are shown in Fig. 7, which represents a longitudinal section considerably off of the median line.

The muscles of the pectoral develop as usual on either side of the coraco-scapular plate *cs*, Fig. 7, and are probably derived as in the Elasmobranchs from buds given off by the muscular segments above the rudiment of the girdle. It will be noticed, however, that there are no muscles developed around or below the yelk-sac, so that there are no recti-abdominales muscles yet formed, the only investment of the yelk being the outer epiblastic covering and the deeper mesoblastic one developed in connection with the vascular net-work which ultimately unites with the heart anteriorly.

Conclusion.—The foregoing account greatly expands and finally completes the history of the development, as far as my materials permit, of this remarkable form, preliminary notices of which I published in *Forest and Stream* in August, 1881, and in the *American Naturalist** for February, 1882. While this history is still far from complete, especially as respects the very early stages, we have at least cleared the ground and prepared the way for further investigations. A number of points which had been left undecided have been determined. These are the following:

1. That fertilization of the egg of *Gambusia* occurs within the ovarian follicle, the spermatic fluid being apparently introduced into the ovary or abdominal cavity by the male, which is provided with an intromittent organ consisting of the anal fin much modified, and that the spermatozoa find access to the egg through a wide opening in the follicle which answers to a micropyle, but which may be called the *follicular pore.*

2. That there is no evidence, as in the case of *Anableps* and the *Embiotocidæ*, that the ovarian follicles are ruptured until the development of the young embryos is approximately completed, since the most advanced fœtuses of *Gambusia* studied by me have the scales, fins, finrays, and cranium remarkably well developed, even before the yelk is all absorbed, as it is known that the young are born not a great while after the stage of development represented in Fig. 3 has been reached.

3. It is also known that little or no nutriment is derived from the parent, as in *Anableps* and the *Embiotocidæ;* or, in other words, that the embryo of *Gambusia* grows entirely at the expense of the material contained in the yelk-sac, and does not form villi upon the latter nor enlarge after the yelk has been absorbed as in *Anableps;* neither does the rectum or hind gut hypertrophy, nor do the fins expand and develop prolongations of the interradial membranes as in the *Embiotocidæ.*

4. As is the case with all viviparous forms, the number of embryos produced seems to be diminished in correlation with the protection which the young receive in consequence of their peculiarly complete development within the body of the parent. The embryos leave the parent as active little fishes about half an inch in length; in fact this fish begins an independent career as far developed as when the shad, cod, Spanish mackerel, catfish, and many other fishes are from three to six weeks old. By so much it has the advantage over those species in the struggle for existence in that it is ready to feed, to pursue its prey discriminately, as soon as it is born, while the other forms alluded to are comparatively helpless until some time after they are born; hence nature makes up in the fertility of such species for the advantages enjoyed by the viviparous ones, so that finally the chances of the survival of the two types, which differ so widely in their breeding habits, are about equal.

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* Structure and Ovarian Incubation of Gambusia patruelis, a top-minnow. Am. Nat., 1882, pp. 109–118.

VI.—HABITS OF GAMBUSIA DURING THE BREEDING SEASON.

Mr. A. A. Duly has informed me that he has witnessed the act of copulation and the birth of the young of *Gambusia*. In coitus the male's head is turned in the direction of the tail of the female, the prolonged anal fin seeming to be thrust into the external opening of the ovarian duct or genital pore of the female, which lies just in advance of the anal fin.

The young when born are stated by Mr. Duly to be about three-eighths of an inch in length, and to be expelled in a single mass, consisting of eight to eleven young fishes at a single effort. This mass as soon as it escapes is seen to be composed of the infant Gambusias, which at once separate and swim away. No membranes seemed to be expelled together with the mass of young, so that it is probable that in this species as in *Anableps* and the *Embiotocidæ* the fœtuses rupture the follicles in which they were developed a short time before birth. I say a short time before birth, because our observations indicate that, unlike *Anableps* and *Micrometrus*, the development of *Gambusia* is essentially completed within the follicles, and no yelk-sac remains outwardly visible when the young are set free.

My informant also tells me that the parent fishes devoured their young as soon as they were born if they were not separated, by transferring one or the other at once to another aquarium. Fright seemed to hasten or precipitate the parturition, which Mr. Duly tells me actually took place under such circumstances. He also noticed that more than one brood seemed to be produced by the same parent consecutively and during the same season, and he has reason to think that more may have been produced, as his observations only extended over the latter part of summer with adults brought from Cherrystone, in August and September, which he kept in aquaria in the National Museum.

VII.—THE VIVIPARITY OF FUNDULUS.

On Plate XI, Figs. 29 and 30, I figure two views of another type of Cyprinodont embryos, viz, *Fundulus majalis*, also obtained at Cherrystone, Va., July 18, 1881. In this case a well-marked *zona* was developed investing the developing embryo. The oil drops were superficially embedded in the yelk the same as in *Gambusia*. A great network of vessels surrounded the yelk, as may be seen in both figures; these spread over the yelk from the two Cuvierian veins which pass out from the side of the body of the embryo just in front of the pectoral fin-folds, and are gathered inferiorly, as represented in Fig. 30, into a great median vein which is extended from the venous end of the heart.

A hood is probably formed at the sides of the head of this species the same as in *Gambusia*, as indicated by the vascular membrane at the sides of the head raised from contact with the yelk, as shown in Fig. 30.

The body cavity under the axis of the embryo is a deep oval sinus extending down a little distance into the substance of the yelk, as shown in Fig 29, behind the rudiments of the pectoral fins.

ON CERTAIN FEATURES OF THE DEVELOPMENT OF THE SALMON.

By JOHN A. RYDER.

So much has been written upon the anatomy and development of this fish by eminent authorities that I approach the subject with a certain hesitancy. The development of the skull has been elaborately worked out by W. Kitchen Parker. The skeleton of the adult has been figured in great detail by Bruch in a magnificent monograph, while the general development has been repeatedly discussed by investigators during the last century with more or less thoroughness. Notwithstanding this, it may be truly said that our knowledge of the exact details of some features of its development is still imperfect, even though such able embryologists as Œllacher, Balfour, His, Hoffmann, and Ziegler have devoted considerable attention to it and its allies within a period extending over scarcely more than the past decade.

The early stages of development have been investigated by Œllacher, His, and Ziegler, with such opportunities that can only be enjoyed by one who is near a locality where the spawning or oviposition of the adults is in progress. I can therefore add nothing to the information given us by those writers, but all that will concern us at present is the arrangement of the blood-vascular system at the time of hatching, some of the impairments which this system suffers when the young fishes are under the care of the fish-culturist, and the development of the fins.

The material used in this investigation consisted of recently-hatched embryos of the land-locked salmon, *Salmo salar*, var. *sebago.* I have carefully drawn a live specimen several times enlarged by the help of the camera lucida, as represented in Fig. 1, in order especially to show the arrangement of the vessels on the vitellus, the distribution of the rose-colored oil drops in the latter, and the vessels and venous sinus in the tail.

The mode of development and outgrowth of the fins is especially interesting, the more so since Professor Cope has recently reached the conclusion that many of the so-called "Ganoids" of the Palæozoic rocks seem really to be affiliated to a great and important order of existing fishes embraced by that author under the term *Isospondyli*, which includes the existing Salmonoids, Clupeoids, Hyodonts, Albulids, &c. As it therefore seems that the salmon belongs to a very ancient series of forms dating back phyletically to the Devonian, it may be well for us to examine into the development of the fins to see if that process would really give countenance to Professor Cope's views.

I. *The vertical fins.*—This set of fins is developed from a median fold extending from a vertical slightly behind the pectorals back over the end of the tail, thence forward on the ventral side to the posterior side

of the yelk-sac, the ventral part of the fold being interrupted only by the posterior part of the gut at *v*. Fig. 1. This fold at the time of hatching contains simple embryonic rays throughout its entire extent, these being indicated in Fig. 1 by the fine linear striation apparent for the whole length of the fold in the engraving. These embryonic rays, as they have been called by A. Agassiz, I will call *actinotrichia*, from their slender, unsegmented, hair-like appearance; they are developed from special cells of the mesoblast, which I have named *pterygoblasts* elsewhere. These actinotrichia exceed in number the permanent rays of the adult at least ten-fold. The latter are in fact in great part formed by the fusion of a number of these actinotrichia lying side by side.

The extent to which actinotrichia are developed in the median fin-fold at the time of hatching, however, varies very greatly in different genera. In the recently hatched salmon, which passes through a prolonged period of incubation, these rudiments of the future permanent rays are very numerous, far more so than is the case with most other forms at the time the embryo escapes from the egg. In the Spanish mackerel and in *Gadus* the actinotrichia are not well defined until some time after hatching, and then only in the posterior end of the median tail-fold and in the pectoral fin-fold. As a rule, actinotrichia, (horny-fibers of Balfour), appear first in the anterior paired fins ; this is the case in the salmon, in which these primitive rays are well marked in the pectoral about the time the ventral fin-folds *vt* become well defined.

As urged in my paper " On the origin of heterocercy," the presence of actinotrichia throughout the whole extent of the fin-folds of the embryos of the salmon is an illustration of the Hæckelian principle, viz, that the ontogeny of a form is usually an epitome of the phylogeny of the same. The persistence of the pneumatic duct and the presence of adipose fins are also to be considered in this connection, since both are archaic characters, the first especially.

The permanent dorsal rays of the salmon are formed from the actinotrichia developed in the anterior part of the median fold *d*, *fig*. 1, towards which radial muscles are shoved out at an early stage, as shown by the evenly stippled intervals at the base of this part of the fold. The fold in the interval between the dorsal and soft dorsal atrophies with the further growth of the young fish, the actinotrichia of this interval also disappearing with the fold.

The next portion *sd* of the median vertical fold which is perceptibly widened, gives rise to the soft dorsal or " adipose fin." The actinotrichia of this fin never pass beyond their embryonic condition, so that it is said by the comparative anatomists to contain horny fibers. The whole of the Plectospondyli except the *Characinidæ* have lost their adipose fins, and thus have but one dorsal remaining. The herrings and salmonoids or *Isospondyli* would therefore seem to stand in an ancestral relation to the carps, suckers, and minnows, or *Plectospondyli*. It is at

any rate obvious that the protopterygian condition of the adipose fin is a less specialized and more archaic one than that of its complete atrophy.

The interval between the soft dorsal and the caudal is in part atrophied. The posterior part of this interval, however, gives rise to the short accessory rays of the dorsal edge of the caudal.

The truly dorsal part of the median fin-fold of the embryo salmon ends at the notch *n*, towards which the urochord, later the urostyle, is directed. At this point the proximal ends of the dorsal and ventral actinotrichia embedded in the fold converge in a penniform manner. The actinotrichia below the notch *n* and extending out into the caudal lobe *cd* give rise to the prolonged caudal rays, while those in the ventral part of the fold just in front of the caudal lobe give rise to the inferior accessory caudal rays.

The fold in the interval between the caudal and anal *a* atrophies, together with its contained actinotrichia, while those in the widened anal part of the fold *a* as far as the vent *v* give rise to the permanent rays of the anal, into which the muscles of the fin grow at an early stage or at about the same time that those of the dorsal are developed.

The prëanal part of the fold *pa* in front of the vent, together with its contained actinotrichia, atrophies entirely during further growth and development.

It is thus shown by the development of the salmon that the most primitive type of distribution of the vertical fins of osseous fishes was a continuous one, because of the development of a continuous series of actinotrichia or primitive rays, and that the forms which now exist and most nearly realize this distribution of the rays of the vertical fins are the Dipnoans, in which the rays are also scarcely more than well-developed actinotrichia, several of which, taken in succession, are homologous with a single ray of an adult Teleost.

The Dipnoans present many other embryonic characters which seem to be partially paralleled by what is transitory in the embryo salmon. When we shall know more of the embryology of *Ceratodus* through the efforts of Mr. Caldwell, who has succeeded in obtaining its ova, further comparisons may be instituted between the ordinary Teleostean embryo and that of the singularly specialized mud-fishes.*

Some of the oldest "Ganoids" had the vertebral axis persistently chordal, unmodified anteriorly, and with an extended series of fins, in these respects paralleling somewhat the condition which is transient in the embryo salmon. These seem to me to be good reasons for accepting Professor Cope's views as to the affiliation of certain of the Palaeozoic fishes with the existing Isospondyli, in the absence, as the latter

* It is important to examine the fin-folds of the tails of the larvæ of such Amphibians as *Pseudis* and *Dactylethra* to determine whether or not actinotrichia are present. Should these earliest representatives of fin-rays be found in any of the Amphibia the abrupt hiatus now existing between the Dipnoans and the latter would, in a great measure, be bridged.

authority states, of all other characters, except the scales, adequate to separate the two.

II. *Paired fins.*—The paired fins of the salmon develop at wide intervals from each other, that is, the ventral pair is separated from the pectoral by an interval of not less than sixteen muscular segments. In *Lophius* the number of muscular segments opposite the interval between the pectorals and ventrals are reduced to four, according to the figures given by A. Agassiz. In other types this interval between the rudiments of the paired fins of the embryo is still further reduced, as for example in *Trachinus vipera** and in *Motella mustela*† in which, according to Brook, but two muscular segments intervene between the earliest rudiments of the pectoral and pelvic fins, so that in these types it may be said that the paired fins develope from almost continuous rudiments. These and *Lophius* seem to develop the rudiments of the paired fins almost synchronously, which is far from being the case with the larvæ of the Physostomous orders, *Ginglymodi*, *Glaniostomi*, *Nematognathi*, *Plectospondyli*, *Isospondyli*, *Haplomi*, and *Enchelycephali*,‡ in which the ventral pair of fins appears late, often after the pectoral is well developed and in active functional use. In most, if not in all, the larvæ of Physostomous species of Actinopteri, as limited by Cope, the ventral pair of fins is later in appearing than the pectoral; on the other hand in the Percomorph and Pediculate divisions of the Physoclistous Actinopteri it seems that in many species the pectoral and ventral limbs appear almost synchronously, the pectoral usually a little more developed than the ventral pair, and separated serially by only two to four myotomes, while this interval in the Physostomous forms may embrace over sixteen muscular segments.

Finally it may be said that the ventral pair of limbs is almost always undergo shifting or translocation forwards in the Physoclistous groups mentioned. The researches of Mr. Brook, cited above, afford additional evidence of the truth of the principle laid down by me in a preliminary notice§ recently published.

The Physoclistous genera, *Gadus*, *Cybium* (*Scomberomorus*) and *Parephippus* seem to be exceptions to the rule spoken of above, as holding in the development of some forms. How far the rule held in the development of the Palaeozoic fishes with ganoid scales and ventral or abdominal pelvic fins, we, of course, now have no means of knowing. These, with the exception of *Dorypterus* and *Blochius*, seem to have had

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*Preliminary account of the development of the Lesser Weever-fish Trachinus vipera, by George Brook, F. L. S., Journ. Linn. Soc., xviii, pp. 274–291, pls. 4, 1884.

†On some points in the development of Motella mustela, Linn., by George Brook, F. L. S., Journ. Linn. Soc., xviii, pp. 299–307, pls. 3, 1885.

‡The eels are of course permanently without ventrals; the youngest obtainable larvæ of Anguillidæ and the Leptocephalid stages of marine eels show no traces of ventral limb-folds; these forms are in fact permanently apodal.

§On the Translocation forwards of the Rudiments of the Pelvic Fins in the Embryos of Physoclist Fishes, Am. Naturalist, 1885, pp. 315–317.

the pelvic fin not displaced forward, but normal in position, as in the majority of existing Physostomous Actinopteri.

The belated development of the pelvic fins of some of the *Isospondyli* and *Haplomi* is quite remarkable; in fact, the pectoral in these forms may have the permanent rays pretty well developed before the ventral fin-fold has done much more than begun to develop. The ventral fin-fold, however, in those forms in which it appears synchronously with the pectoral is at first always the smallest, thus showing the effects of an inherited tendency to retard the development of the pelvic fins.

In the salmon the pectoral is functionally developed with well defined actinotrichia lying beneath the investing epidermis, as shown in Fig. 1, by the time the ventral is appearing as a flat, immobile lobe without developed actinotrichia, behind and above the yelk-bag.

III. *The embryonic blood vascular system.*—In the embryo salmon this attains great importance apparently in consequence of the presence of a voluminous yelk which is absorbed by a system of vitelline vessels. A large median aortic trunk *ao*, Fig. 3, is developed under the notochord *ch*, Fig. 4. It is formed from two convergent suprabranchial arteries anteriorly, which receive their blood from the branchial trunks coming from the gills. The aorta extends backward, giving off "intercostals" and intersegmental branches *s* along either side and terminates under and at the end of the urochord. A recurrent vessel then bends down from it and divides into several loops which converge in the caudal venous sinus *sc*, Fig. 3, incorrectly referred to as a "caudal heart" by some writers, as it exhibits no independent pulsations of its own.

From the caudal sinus the caudal vein or cava arises and passes forward towards the body-cavity, where it divides anteriorly into the paired cardinal veins *cr*, Fig. 3. These pass forward to the venous sinus of the heart formed by the Cuvierian ducts into which they empty their contents. The heart lies behind and below the branchial frame-work, and forces only venous blood through the gills. Its anterior chamber or bulbus aortæ is prolonged forward into a truncus arteriosus, which gives off a pair of vessels to each pair of gills. These vessels, after breaking up into a plexus of capillaries, send the arterialized blood through another set of branchial vessels which join a pair of longitudinal trunks, of which the radices aortæ are prolongations posteriorly and the carotids anteriorly. The venous blood from the head is carried back to the heart by way of a pair of jugular veins or anterior cardinals to the venous sinus. The foregoing describes in outline the systemic circulation proper, exclusive of the great portal system, to which the network covering the yelk-bag also properly belongs.

The portal system of the young salmon with the yelk-bag still attached may be said to comprise no less than three successive sets of capillaries. The first of these arise from the caudal and cardinal veins *cr*, and pass from above downward on either side of the intestine to join and fill with blood a large azygous or median subintestinal vein,

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si, Fig. 3. This vessel passes forward under and into the liver *L*, where it again breaks up into a plexus of smaller vessels; these then again blend into larger trunks, as shown at *pv*, in Fig. 4, which emerge from the liver to again break up into the capillary net-work *cc*, Fig. 3, which is still better shown in Fig. 1, on the surface of the yelk-bag. This vitelline net-work then joins the vitelline veins *vv* and *vv′*, which blend into a common trunk before joining the venous end of the heart. It will thus be seen that we have no less than five capillary systems in the young salmon, as shown in Fig. 1, if we reckon those of the portal system together with those belonging to the systemic system of vessels. These in their order are: (1) The branchial, (2) the systemic, (3) the intestinal, (4) the hepatic, and (5) the vitelline capillaries.

What the subsequent history of the third and fourth sets may be I have not made out, but the fifth or vitelline set has only a temporary existence, remaining only as long as there is yelk in the yelk-bag. As the yelk is absorbed this system disappears, when the vitelline veins *vv* and *vv′* become portal veins; that is, they carry all of the blood which passes through the viscera back to the heart.

A study of sections of the yelk-sac of the salmon leads to the following conclusions: A well-marked periblastic stratum of plasma, *p*, Fig. 4, invests the yelk. Beneath the periblast lie the oil-drops *o*, *o*, which are largest at the upper part of the yelk, the greater buoyancy of these larger, superior oil globules tends to keep the young fish buoyed up, and functions much in the same way that an air bladder would, a structure which, by the way, is not yet functional in the young salmon at this stage of growth. In the earlier stages these larger oil-drops, which lie just under the blastodisk or germinal mass, by their buoyancy constantly keep the germ rotated or turned toward the top of the egg.

External to the periblastic layer of the yelk comes the vascular net-work of capillaries, the walls of which are formed, apparently, by a thin sheet of splanchnic mesoblast *vm*, which invests the yelk but which has grown down over the latter at a later period, possibly, than the thin epidermic or epiblastic investment *ep*, Fig. 4. This vascular net-work is obviously the apparatus by means of which the yelk is absorbed superficially from the external plasmodium or periblast of the yelk, a stratum, which, as is well known, contains scattered free nuclei.

The epidermis or epiblast of the young salmon is remarkable amongst fish embryos for the peculiar goblet-shaped cells which are found distributed over almost the entire surface of the embryo. These are shown in a section of the epidermis in Fig. 5, much enlarged. Their function is apparently to secrete a mucilaginous substance for the purpose of protecting the skin of the embryo.

IV. *Diseases or abnormalities which involve the yelk-sac and vitelline*

circulation of salmon embryos.—A discussion of some of the pathological phenomena observed while salmon embryos are under the care of the fish-culturist seem to me to be in place here.

Shortly after hatching many of the young fish in the hatching troughs sometimes show whitish spots on the yelk-sac. If examined under the microscope it is plain that these spots consist of coagulated or dead yelk material. Very often the capillaries in the vicinity of these spots are found to be occluded and filled with clots of blood, as if the vessels had been bruised. In other cases it is found that the capillaries of the liver are occluded so that that organ, which is visible on the left side of the embryo through the integument, assumes a whitish, abnormal color. Closer examination reveals the fact that the blood no longer circulates through the liver, and that the tissues of the organ are practically dead, as indicated by the white color which they assume. These conditions lead to the death of the affected embryos in great numbers. The causes which seem productive of such abnormalities have not been determined with certainty, but it would seem probable that blows or knocks received by the sac from careless handling or the violent and too rapid flow of water over the young fish, so as to carry them violently against fixed objects in the trough, are probably very hurtful and productive of the changes noted.

Still other abnormal changes in the yelk-sac may be noticed here. The most serious is that characterized by the distension of the epiblastic covering of the sac with fluid so that it is lifted up from contact with the yelk more or less extensively. Usually, this distension only affects the posterior extremity of the sac, but occasionally specimens are observed in which there is a space all round the yelk between the latter and the epiblastic sac. Sometimes free-blood corpuscles which have escaped from ruptured vessels are found floating about in the fluid contained in the cavity described. At other times, an extension of the back part of the yelk proper may be prolonged backward into the outer sac, which may become constricted so as to embrace part of the yelk. As the anterior part of the yelk is then absorbed, the posterior constricted part is finally left hanging to the abdomen by a sort of pedicle formed by the outer sack. This finally drops off and the young fish survives. The spot where the stalk breaks off on the under side of the embryo heals up and the young fish seems none the worse for having lost part of its yelk, except that it has probably not grown quite so large or so rapidly as its more fortunate fellows.

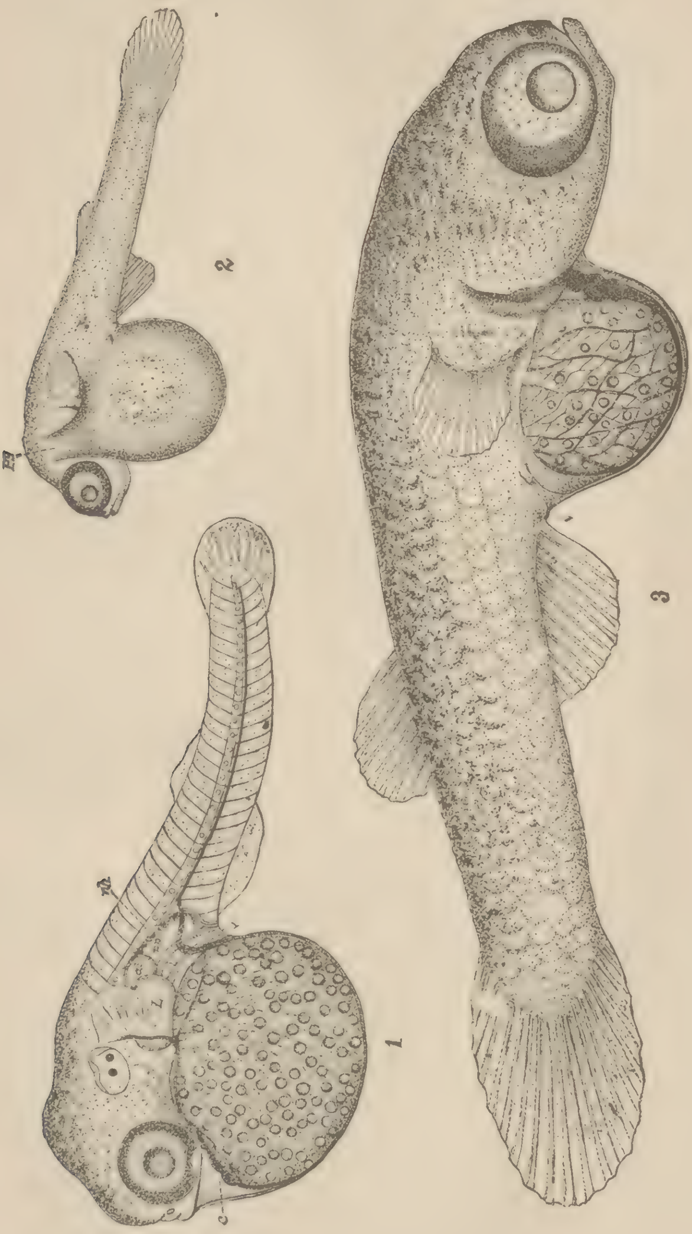
The plate illustrating the foregoing article is number XII of the present volume.

EXPLANATION OF PLATE VI.

FIG. 1.—Side view of fœtal *Gambusia* recently removed from the ovarian follicle. x 22.

FIG. 2.—Side view of a somewhat older embryo taken from the follicle and hardened in chromic acid. x 11.

FIG. 3.—Side view of a still older embryo, with the yelk-sac still apparent, taken from the follicle and figured while alive. x 22.



DEVELOPMENT OF GAMBUSIA PATRUELIS.

EXPLANATION OF PLATE VII.

REFERENCES:—*a*, anal fin; *ab*, air-bladder; *al*, urinary vesicle; *au*, auditory vesicle; *ba*, bulbus aortæ; *c*, pericardiac cavity; *cs*, coraco-scapular cartilage; *f*, pecten; *i*, intestine; *L*, liver: *m*, muscular somites; *mb*, mid-brain; *Mk*, Meckel's cartilage; *n*, nasal pit; *o*, generative gland; *pn*, mesonephros: *pq*, palato-quadrate cartilage; *pp*, peritoneal cavity; *r*, muscles of the eye: *sc*, cavity between the viscera and yelk; *sv*, sinus venosus; *v*, vent or anus; *vv*, vitelline vessels; *ve*, ventricle: *Wd*, Wolffian or segmental duct; *y*, yelk; *yh*, yelk hypoblast or periblast.

FIG. 4.—Fœtus hardened, in its follicle to show the way in which it is coiled up. x 15.

FIG. 5.—Transverse section of an advanced embryo through the yelk-sac and body in the vicinity of the pectoral fins. x 29.

FIG. 6.—Longitudinal vertical section of an advanced embryo somewhat off of the median line. x 29.

FIG. 7.—Longitudinal vertical section of a similar embryo nearer the median line than the preceding, x 29.

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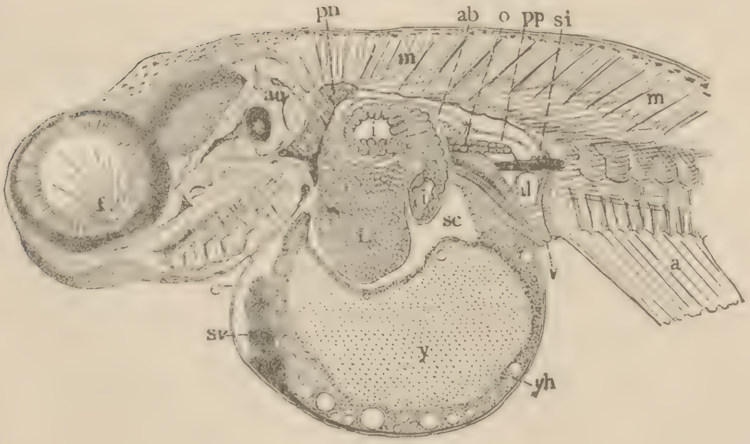

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DEVELOPMENT OF GAMBUSIA PATRUELIS.

EXPLANATION OF PLATE VIII.

REFERENCES: *ab*, air-bladder; *ao*, aorta; *au*, auricle; *ba*, bulbus aortæ; *ch*, chorda dorsalis; *ep*, epiblast of yelk-sac; *fm*, follicular membrane; *fv*, follicular vessel; *i*, intestine; *L*, liver; *mp*, follicular pore; *ms*, medulla spinalis; *pf*, muscular mass at base of pectoral; *sv*, sinus venous; *t*, pectoral in section; *vc*, venæ caudalis and cardinales; *ve*, ventricle; *Wd* Wolffian duct; *y*, yelk; *yhy*, yelk hypoblast or periblast.

FIG. 8.—Transverse section through the heart, showing its chambers. x 35.

FIG 9.—Transverse section through a follicle containing an embryo, cutting through the plane of the follicular pore. x 32.

FIG. 10.—A follicle containing an embryo with two immature eggs attached near the follicular pore. x 15.

FIG. 11.—Ovary of *Gambusia*, showing the way in which the ripe ova are attached to the median vessel. x 3.

FIG. 12.—Follicular pore and adjacent parts of membrane of a follicle, showing the course of the vessels, from a transparent preparation in balsam. x 65.

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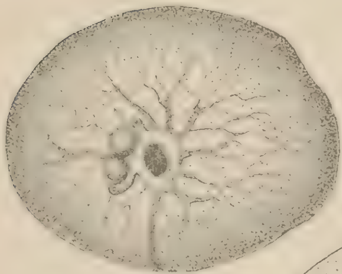

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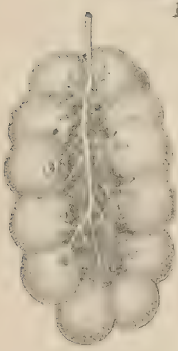

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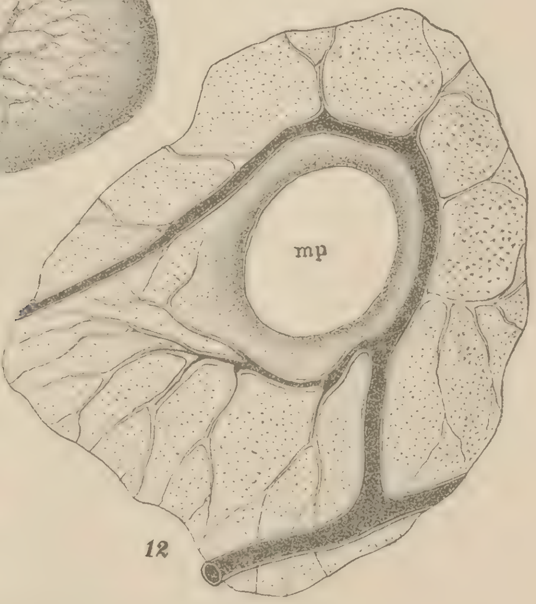

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DEVELOPMENT OF GAMBUSIA PATRUELIS.

EXPLANATION OF PLATE IX.

REFERENCES: *a*, anal fin; *ab'*, branchial artery; *b*, basicranial end of chorda; *bh*, branchial arch; *c*, cartilaginous axis of branchial filament; *ch*, chorda dorsalis; *e*, end organs or neuromasts on the cheeks; *hs*, hæmal cartilages; *l*, intervertebral ligaments; *ms*, medulla spinalis; *n*, nerves to neuromasts; *ns*, neural spines; *r*, rays; *rb*, rib; *sh*, membranous basis of vertebral centrum; *sp*, scale pouches; *u*, hæmal cartilage into which the urochord projects; *vr*, vertebral centra; *vt*, ventral fin.

FIG. 13.—Earliest embryo of *Gambusia* as it lies in the follicle. x 22.

FIG. 14.—Part of follicular membrane very much magnified. x 365.

FIG. 15.—Cross-section through the tail of an advanced embryo. x 35.

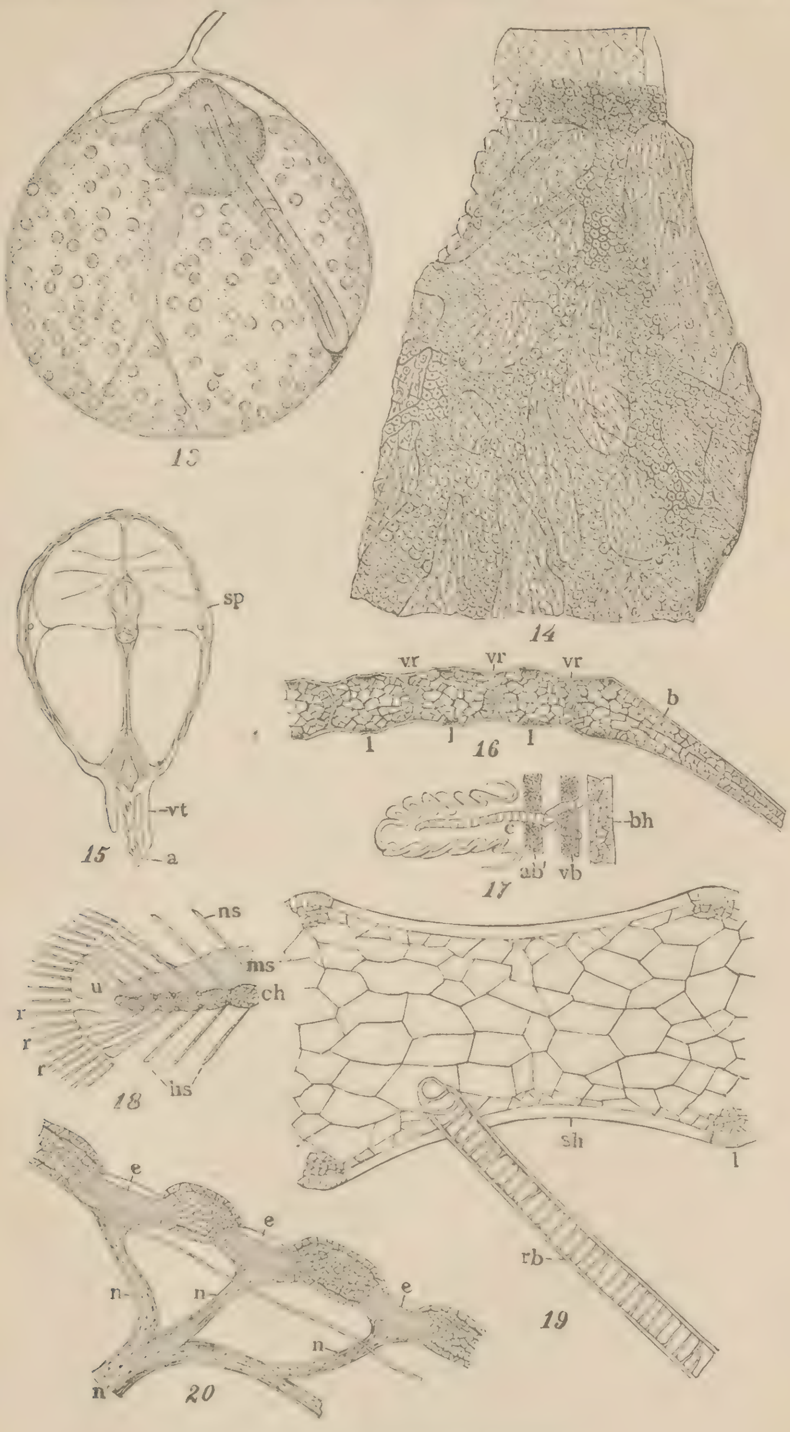
FIG. 16.—Longitudinal section through the anterior end of the incipient vertebral column of an advanced embryo. x 96.

FIG. 17.—Longitudinal section through a branchial filament. x 183.

FIG. 18.—The tail of an advanced embryo, drawn from sections. x 35.

FIG. 19.—A vertebral segment and rib in place, from an advanced embryo. x 365.

FIG. 20.—Neuromasts with their nerves from a cross-section through the cheek of an advanced embryo. x 200.



DEVELOPMENT OF GAMBUSIA PATRUELIS.

EXPLANATION OF PLATE X.

REFERENCES: *ab*, air-bladder; *ao*, aorta; *Au*, auditory vesicle; *B. B*, basibranchial cartilages; *Br*, branchial bar; *Brs*, branchiosteges; *Cb*, cerebrum; *Cer*, cerebellum; *ch*, chorda; *Ch*, optic crus; *Chs*, chorda sheath; *Cor*, coracoid end of scapular arch; *d*, denticles; *df*, dental follicle; *Dm*, dermal muscle; *ep*, epithelium; *F*, cranial fontanelle; *Ghy*, glosso-hyal; *Hi*, hypophysial involution; *Hm*, Hyomandibular; *Hy*, hypophysis; *H. Hy*, Hypo-hyal; *i*, intestine; *I. H*, interhyal; *In*, infundibulum; *it*, *iter a tertio*; *m*, myotomic segments; *mb*, mid-brain; *me*, mesoblast; *mes*, mesentery; *Mk*, Meckel's cartilage; *ms*, medulla spinalis; *nc*, canalis centralis; *ns*, cartilaginous or fibro-cartilaginous neural arch; *o*, genital folds; *oep*, oral epithelium; *Oc*, occipital cartilage; *Or*, orbit; *Om*, ocular muscles; *pp*, peritoneal cavity; *pp′*, peritoneal or lymph cavity on either side of the air-bladder; *pi*, pigment layer; *Pch*, parachordal element; *pch*, perichondrium; *Pr*, Pons varolii; *Pn*, mesonephros; *pn*, pineal gland; *P. Pt*, palato-pterygoid; *Qu*, quadrate; *r′*, *r′*, rays; *rb*, cartilaginous axis of ribs; *rb′*, fibro-cartilaginous investment of ribs; *rao*, radix aorta; *s*, perichondrial tooth-sockets (cementum plates of pharynx); *Sc*, scapular part of shoulder girdle; *S. br*, supra-branchial elements; *Sk*, skeletogenous tract from which the vertebræ and arches develop; *ssv*, supra-spinal vessel; *sl*, deep layer of epidermis; *Sy*, symplectic; *Tr*, trabecula (anterior part); *T. cr*, tegmen cranii; *vc*, vena cardinales; *Wd*, Wolffian ducts.

FIG. 21.—Chondrocranium of advanced embryo of *Gambusia*. x 35.

FIG. 22.—Cross-section through chorda, medulla and incipient vertebræ of the tail. x 65.

FIG. 23.—Cross-section through an embryo of *Gambusia* just behind the occiput. x 65.

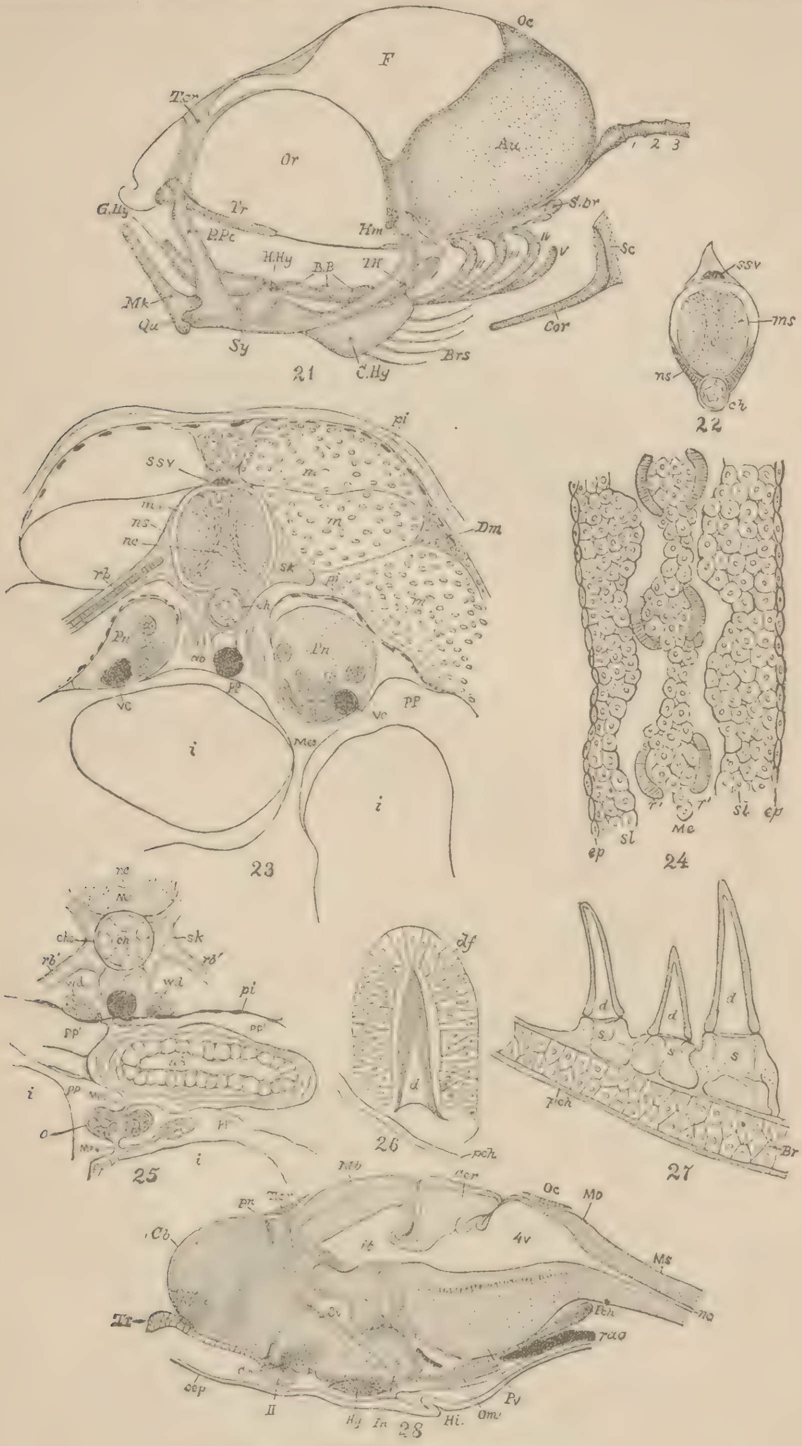
FIG. 24.—Cross-section through the tail of a similar embryo. x 365.

FIG. 25.—Cross-section through the posterior part of the air-bladder and adjacent organs of an embryo of *Gambusia*. x 96.

FIG. 26.—Section through a dental follicle and tooth from the pharyngeal region. x 365.

FIG. 27.—Section through a group of pharyngeal teeth and their supporting plates and branchial bar. x 365.

FIG. 28.—Median section through the brain of an advanced embryo of *Gambusia*. x 35.



DEVELOPMENT OF GAMBUSIA PATRUELIS.

EXPLANATION OF PLATE XI.

FIG. 29.—Transparent view of a developing ovum of *Fundulus* forced from the ovary by pressing the abdomen of the living fish. x 32.

FIG. 30.—A similar view of another ovum of the same species; the embryo viewed from below and anteriorly, instead of from above, as was the preceding. x 32.

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DEVELOPMENT OF FUNDULUS.

EXPLANATION OF PLATE XII.

REFERENCES: *a*, anal lobe; *ao*, aorta; *c*, vitelline capillaries; *ca*, carotid; *cd*, caudal lobe; *cv*, cardinal or caudal vein; *ch*, chorda dorsalis; *d*, dorsal lobe; *ep*, epiblast of yelk-sac; *g*, goblet cells of epiblast; *h*, heart; *i*, intestine; *j*, jugular; *L*, liver; *ll*, lateral line; *m*, cut ends of dorsal halves of the muscular segments; *ms*, medulla spinalis; *n*, caudal notch; *o*, round spaces in sections of vitellus in which oil has been contained; *p*, periblast; *pe*, pectoral; *pv*, portal vessel, prëanal lobe; *r*, ribs, cut through obliquely in the section; *s*, segmental intermuscular vessels; *sc*, caudal sinus; *scl*, subclavian artery; *sd*, soft dorsal lobe; *si*, subintestinal vessel; *v*, vent; *vv* and *vv'*, vitelline veins; *vc*, venæ cardinales; *vm*, mesoblastic investment of vitellus; *vt*, ventral fin; *Wd*, Wolffian duct.

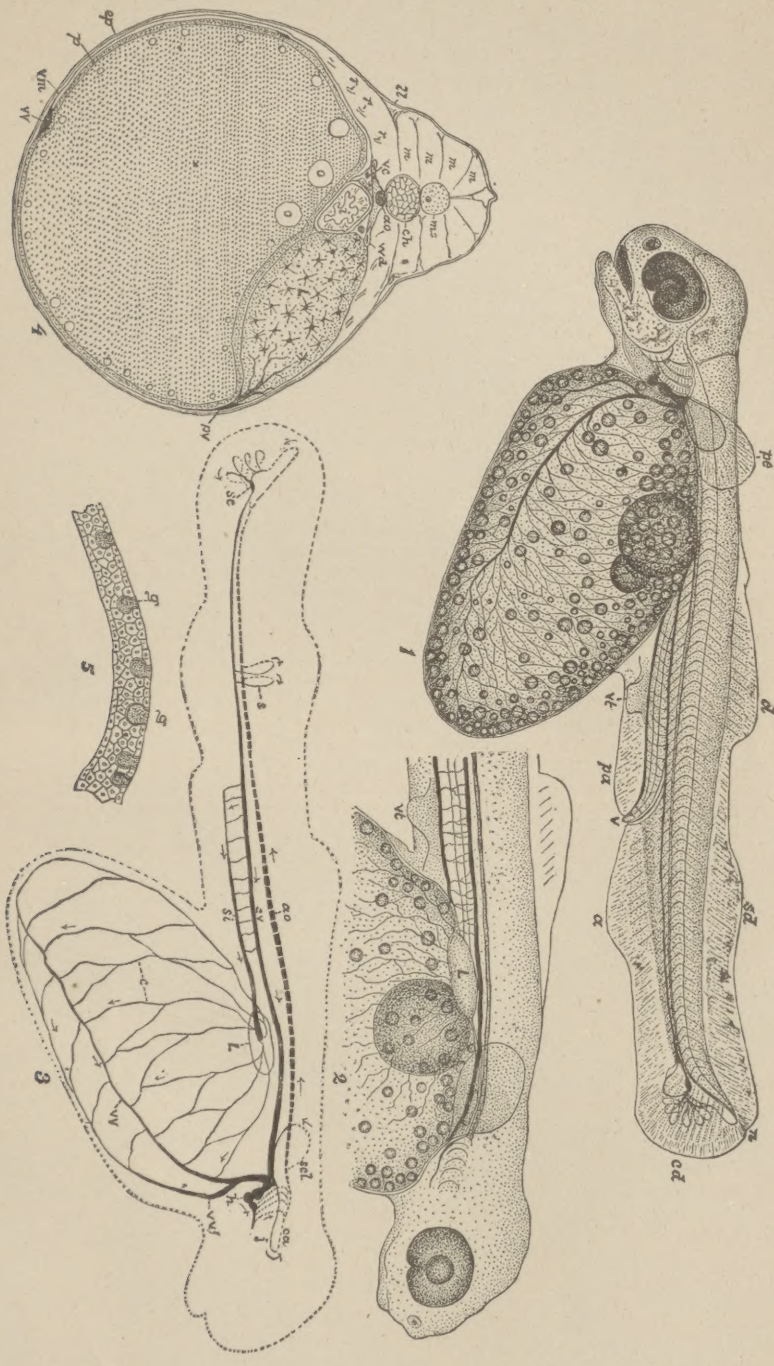
FIG. 1.—Recently hatched embryo of the Schoodic or landlocked salmon, viewed from the left side and figured from the living specimen. x 7 +.

FIG. 2.—Same viewed from the right side. x 7 +.

FIG. 3.—Diagram of the circulatory system of the young salmon.

FIG. 4.—Cross-section through the body and yelk of a young salmon, through the region of the liver. x 16.

FIG. 5.—Section through the epidermis of a salmon embryo to show the goblet cells *g*. x 200.



CERTAIN FEATURES OF THE DEVELOPMENT OF THE SALMON.